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Dispersion of Small Organisms*

Incidence of Viruses and Pollen; Dispersion of Fungus Spores and Insects

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CONTENTS

Since an earlier publication on the subject of dispersion of small organisms, Wolfenbarger (1946), a decade ago, many authors have published on their findings. Except for a few brief references to reports treated in the earlier publication most are omitted here, although publications previously unknown or unobserved are included in this paper. It is the aim to continue descriptions of dispersion or incidence as affected by distance in quantitative and objective terms. Although most references cited give results that are quantitative in terms, certain few references present discussions that are qualitative in character. Methods, organization of materials, and procedures previously used are continued. Part I of this publication is devoted to graphic illustrations showing distances to which organisms disperse or are dispersed or the distances to which incidences of disease, infestations

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occurrences or injuries were determined. By means of the graphs, interpolations may be made easily, considerations may be given to variations in observed and curve values, and extrapolations may be made. References to inanimate objects are given first, followed by the lower, then more complex forms of life terminating in references to the specialized forms of the Class Insecta. Dispersion is discussed under two headings, depending on whether it is horizontal or vertical. Generalizations are given in Part 2.

Dispersion is the general exodus, scatter, or emanation of organisms from the source. Frequently definite and separate activities are exhibited in the dispersion process. A term often used instead of dispersion is migration. Although the two terms have the same general meaning, migration implies a return trip and also group movement. Actually return trips of some organisms do occur: an example being the bogong moth, *Agrotis infusa* (Boisd.), as reported by Common (1954). Group movement is also frequently observed. It is considered essential, however, that return trips or group movements should be in evidence in order to use the term migration. Most small organisms tend to move away from the origin, although over wandering paths that may cross and recross. Such movements are responses of individuals, unrelated to return trips or group movements. The evidence also indicates that individuals may follow paths that are separate from those of other individuals. Definitions and concepts adopted in the previous publication, Wolfenbarger (1946), are used without significant change.

Although different regression formulae have been used by other authors, those given by Wadley and Wolfenbarger (1944) were retained. Since no simple formula will be suited to all data on dispersion or incidence and since these formulae have been generally satisfactory they have been employed. Other regression formulae, as phrased by Gregory and Read (1949), ". . . . could have been fitted equally well; that is, there would have been no statistically significant departure from any one of certain other relationships, ..." This is especially true where observed data comprise but few (3–5) pairs of observations. Further improvement is sought by Wadley (1957), as ". . . more and better data are needed."

Data on dispersion ordinarily show curvilinear relationships by plotting unit and distance figures. By changing distances to logarithms, however, straight-line relationships become evident. In this paper the regular regression formula was used wherever a straight-line was indicated by preliminary plotting: except that the distance values were converted to logarithms. This is given as

$$E = a + b\ (\log x).$$

Wherever the data showed curvature after logarithmic transformation a modification was made in the above formula. This modification added the reciprocal of distance and required an additional computation. Two allowances were provided for distance, according to Wadley (1957), in which "$b \log x$ (b negative) is to represent the dropping out, and c/X the hyperbolic effect expected from thinning out." This is the modified formula,

$$E = a + b\ (\log x) \div c/x,$$

where "E" refers to the "expected", "calculated", "theoretical" or curve values. It is measured on the y-axis as the dependent variable. The "a" is for position and is dependent on the data in each problem. The symbols "b" and "c" are factors obtained from the data and are used for determining the slope of the curve. The "x" refers to distance and is the independent variable. Distances or x-values were transformed to logarithms for computing the various regression formulae as given in the Appendix. Since the distance values were known, given as a part of the problem, there is no need for re-transformation after completion of the computations by the above formulae.

Salt deposits are inorganic materials and obviously are dispersed by wind or other agent. Viruses and pollen may not be comparable to organisms but depend on energy from an outside source for their dispersal. They are included under the above title and in the discussion because of their relationships and interest to the subject. Knowledge of dispersion of these materials contributes to greater understanding of organismal dispersion.

ACKNOWLEDGMENTS

Grateful appreciation is expressed to Dr. L. A. Hetrick, Associate Professor, Department of Entomology, College of Agriculture, University of Florida, and to Dr. E. G. Kelsheimer, Entomologist, Gulf Coast Experiment Station, Florida Agricultural Experiment Stations, University of Florida for reading the manuscript and for the improvements they suggested in reference to it. I also wish to thank the Foundation for Microbiology, Rutgers University, New Brunswick, N. J. for the grant received to defer the cost of publication of the numerous illustrations.

Dispersion and Incidence Rates, Part I

HORIZONTAL DISPERSION

Inanimate Materials

Salt spray deposits.—Through the use of cheese cloth traps Boyce (1954) determined the average deposits of salt at distances from mean tide levels. Deposits were also determined at different wind speeds. Four regression curves, however, were drawn to show salt deposits as affected by distance (Fig. 1). Low salt deposits were reached at 50–100 meters at low wind speeds. High wind speeds carried salt water to distances in excess of 300 meters. There is fair agreement of observed and curve values. Considerable economic importance may be attached to the dispersion of salt water along the shore. This is especially true where it is desired to raise plants that are susceptible to chloride injury. Further reference is made to this article under "Wind Speed" of Generalizations.

Unknown or Virus

In their studies on the clove tree, Nutman and Sheffield (1949) reported on "Life expectancy" of trees with "sudden death". Life expectancy was computed for trees near the source as compared with the life expectancy of trees further away. Cause of death is not known but may be attributed to cultural conditions. Distances from early

affected trees were related to dying as shown in Fig. 2, although monthly intervals also influenced the time of death. Life expectancy was almost one-third greater at five tree intervals than for trees adjoining diseased trees. Rate of spread expressed by the authors was ". . . of two tree intervals every nine months." Although the semi-logarithmic formula was used for calculating the expected values (Fig. 2), non-transformed data would given a very satisfactory agreement of regression and observed values. Means of dispersion is not known.

The Eastern x-disease of peach spreads readily from chokecherry to peach but not from peach to peach according to Stoddard (1947). He found more diseased plants in a nursery nearest chokecherry plants than at more remote distances. A regression curve from data given by Stoddard (1947) was drawn to show the incidence rate (Fig. 3). The curve reached zero per cent infected plants at near 190 feet from the chokecherry plants. All plants within about 50 feet of chokecherry plants would be infected with the x-disease according to the curve. Means of spread is by certain leafhoppers, *Callodonus clitellarius* (Say).

The degree of isolation of cabbage seed-beds from seed fields was found by Pound (1946) to have influenced the percentage of plants infected with mosaic disease. From the data given, a regression curve was drawn (Fig. 4). High percentages of infected plants were found at 20 and 200 rods. Very low percentages of infected plants were found at 7 and at 20-plus miles from seed fields. Observed and curve values lack close agreement at the two greatest distances that observations were made. The virus inoculum is spread by means of the winged form of the cabbage aphid, *Brevicoryne brassicae* (L.), which infests beds nearest the seed fields more abundantly than the more distant beds.

Incidence of a mosaic disease of the garden beet, *Beta vulgaris* L., depended on its isolation from steckling beds, as reported by Pound (1947). Isolation distances of 0.125, 0.750, and 6.000 miles were taken for the given degrees of, "less than ¼ mile", "less than 1 mile" and "more than 5 miles", respectively. Averages of the percentages of plants infected from the fields in each distance class were used for determination of a regression curve (Fig. 5). An expected 12 percent infection was computed for the six-mile distance where plants at the zero distance were 100 percent infected. Isolation was the recommended control through, ". . . growing steckling beds in sections well isolated from disease seed fields." Spread of the virus was believed accomplished by the black bean aphid, *Aphis fabae* Scop. and the green peach aphid, *Myzus persicae* (Sulz.).

Wheat streak virus was found to be transmitted to healthy plants by the eriophyd mite, *Aceria tipulae* Keifer. More plants with virus symptoms were found nearer the inoculum source than at more remote distances. The incidence of disease was found much greater, however, in laboratory tests by Slykhuis (1955) where a fan dispersed mites carrying the inoculum. Incidences were measured to 12 feet from the source. Two regression curves were drawn to show the distance relationships (Fig. 6 and 7). The operation of a fan made wide differences in the incidence of disease. All plants to distances of four

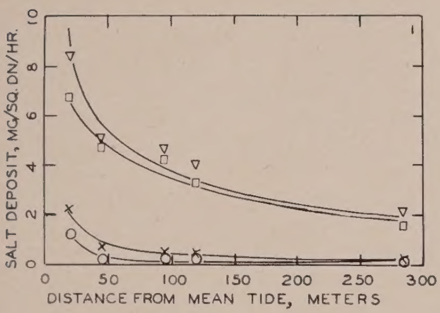

Fig. 1

Incidences of salt deposits at distances from the sea coast. Curves from lowest to highest positions represent different wind speeds, 2.5, 5.5, 8.0 and 11.0 meters per second, respectively (data from Boyce).

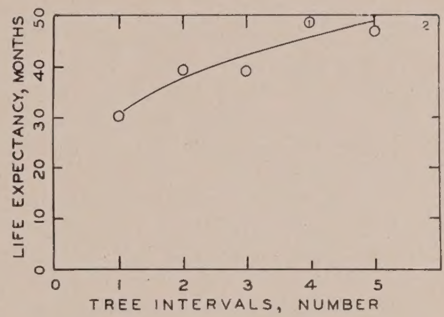

Fig. 2

Life expectancy of "sudden-death" of the clove tree (data from Nutman and Sheffield).

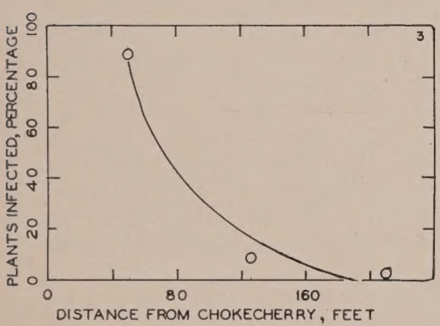

Fig. 3

Incidence of the Eastern x-disease of peach as related to the distance from chokecherry plants (data from Stoddard).

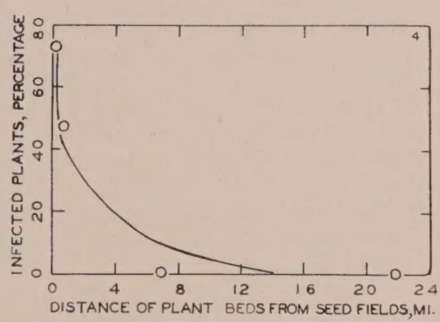

Fig. 4

Incidence of mosaic infected cabbage plants in seed beds at distances from seed fields (data from Pound).

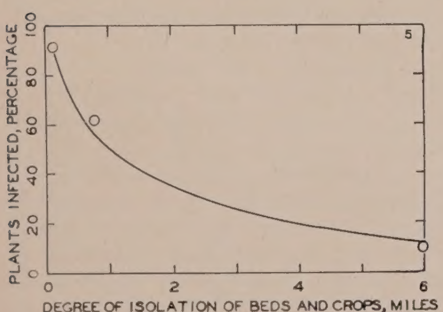

Fig. 5

Incidence of beet mosaic infected beet seed as related to distance from steckling beds (data from Pound).

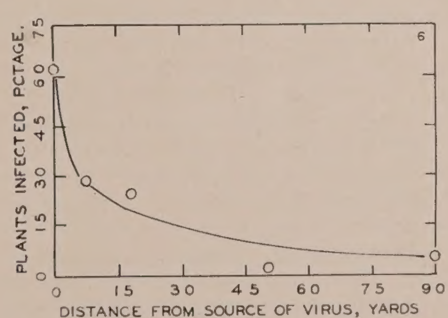

Fig. 6

Incidence of wheat streak mosaic disease at distances from infected plants, field study (data from Slykhuis).

feet from the inoculum source were infected where a fan, mites, and diseased plants were present. Low incidences of disease were found within four feet where no fan was in operation. No infected plant was found where mites were present and a fan was operated but where no virus inoculum was present. No transmission occurred where mosaic was present and a fan was in operation but where no mites were present.

Incidence of wheat streak virus was also tested by Slykhuis (1955) under field conditions. Plants were exposed for a week at distances from a source during the months of August, September, October, and November. Averages of the data given for each distance class of all exposures were obtained and used for computing a regression curve (Fig. 6). Over 60 percent of the plants nearest the inoculum source were infected whereas at 50 feet the regression curve shows about 10 percent and at 90 feet an incidence of near 5 percent infection is indicated.

Incidence of mild streak of black raspberries was related to the proximity of wild or escaped bramble plants, according to Jeffers and Woods (1948). They took data over a six-year period, 1942 through 1947. A regression curve was drawn to show the incidence of disease for each year (Fig. 8). A very low incidence of disease existed in 1942, even on plots nearest the wild brambles. Markedly greater percentages of diseased plants were found 25 feet from the source of the virus than 75 feet away in 1943 and through 1947. Infections became 100 percent adjoining the wild or escaped plants, but required five years to reach 80 percent at 125 feet from the source. Further reference is made to this study under Generalizations. The means of dispersion of mild streak inoculum is not known but its transmission is presumed to be by insects.

Statistical analysis of data on spread or rugose mosaic and potato leaf roll diseases among healthy potatoes were made by Gregory and Read (1949) over a four-year period. They found that differences between years and between diseases were greater than could be accounted for by chance occurrences. The incidence of rugose mosaic disease as affected by distance from the inoculum source for each of the four years is given in Fig. 9. Rather similar rates of incidence were found for each of the four years. Incidence of the disease extended to some distance beyond the maximum observed distance, 90 inches. Means of dispersion of the rugose mosaic inoculum is by insects.

Incidence of potato leaf roll disease infections were studied by Gregory and Read (1949), for distances to 90 inches from the diseased plants. Results of four years observations are given in Fig. 10. Although incidence of the disease was very markedly reduced within a distance of 90 inches, there were differences between years. Rather similar rates of curvilinearity were found, however, for each of the four seasons. Means of dispersion of leaf roll inoculum is by insects.

Plant spacing as a means of potato leaf roll control was tried by Bawden (1951) who spaced plants 9, 18, and 35 inches from the inoculum source. A regression curve was drawn from the data given (Fig. 11). A rapid decrease in leaf roll infections was found between 9 and 36 inch spacings. A low percentage (two) of diseased plants was found at the 36 inch spacing from the virus source.

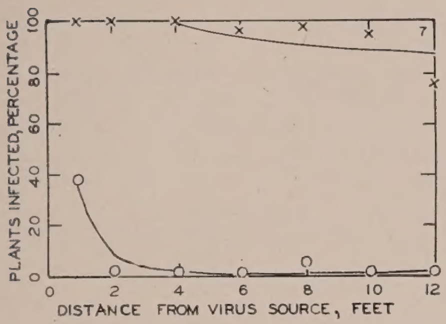

Fig. 7

Incidence of wheat streak mosaic disease, Laboratory study.

Upper curve represents mosaic source, mites and fan present.

Lower curve represents mosaic source, mites (no fan) present (data from Slykhuis).

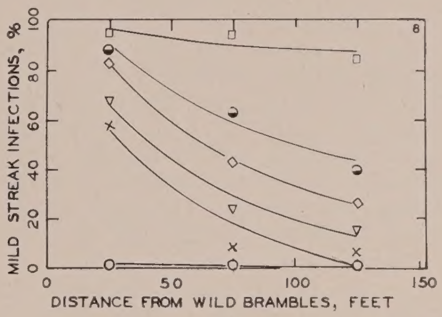

Fig. 8

Incidence of mild streak disease of black raspberries.

Lowest curve represents data taken in 1942, successively higher curves represent data through 1947 (data from Jeffers and Woods).

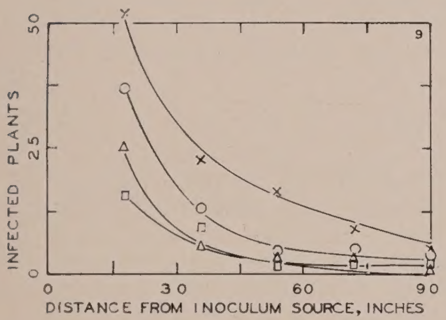

Fig. 9

Incidence of rugose mosaic disease at distances from infected potato plants. Different curves represent data from different seasons (data from Gregory and Read).

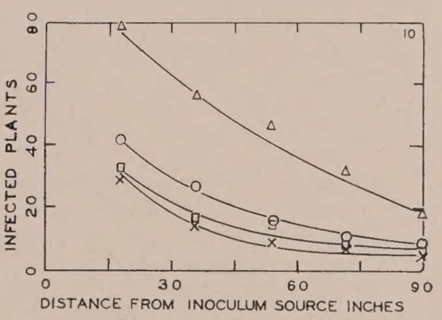

Fig. 10

Incidences of potato leaf roll infections at distances from diseased plants. Different curves represent different seasons (data from Gregory and Read).

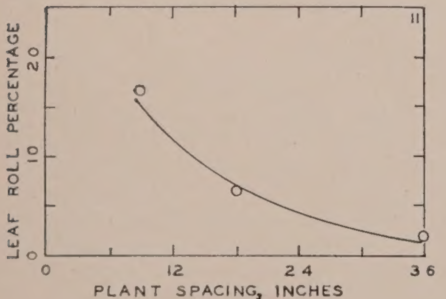

Fig. 11

Potato leaf roll disease incidence as affected by plant spacing (data from Bawden).

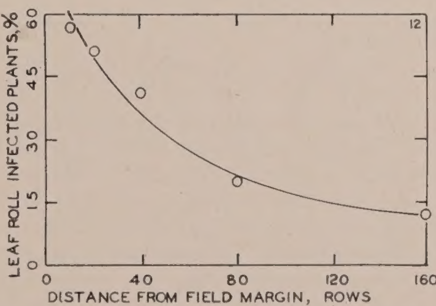

Fig. 12

Incidence of potato leaf roll disease at distances from a field of late potatoes (data from Klostermeyer).

Potato leaf roll disease was found closely associated with the number of aphids present. Dispersion of viruliferous aphids from a field of early potatoes was found by Klostermeyer (1953) to be inoculating healthy plants in a field of late potatoes. A curve was drawn to show the rate of infected plants affected by distance from the field of early potatoes (Fig. 12). Distances in terms of "rows" were used for measuring the rate of inoculation. If three feet is taken as the distance between rows infected plants were found to distances of 480 feet from the field margin of the late potato planting. There is fair agreement of observed and curve values. Potato leaf roll inoculum is spread by aphids.

Spread of tristeza disease of citrus was studied by Bitancourt and Rodriguez (1948). They took data of spread on three occasions. Some secondary or later spread may have influenced the results on the last two or three count days. If so, however, the results were apparently not greatly altered. A curve was drawn from averages of a combination of all data (Fig. 13).

General decreases in disease were found to distances of 75 feet from the inoculum source. Only fair agreement of observed and curve values was found. It is clear, however, that infections occurred at distances in excess of 75 feet. Aphids are believed to disperse the inoculum.

Kingdom Plantae
Fungi

Airplane flights over Arctic and sub-Arctic regions were made for the purpose of collecting spores. Greased slides were exposed at different degrees of latitude for five-minute periods. Spores of plant disease fungi, especially those producing rust and smut of cereals, were taken over northern regions of the North American continent. Regression curves were drawn from data given by Pady et al. (1950) and are shown in Fig. 14. Air-borne spores decreased with increases in latitude northward. Most spores were collected and most fungus colonies developed on slide exposures made at latitude 57° 30′. This latitude was nearest the sources of spore production. The spores collected and the number of colonies per plate were much fewer at the greater latitudes than at the spore source. Means of dispersion was by wind.

Studies on incidence of damping-off disease were reported by Blair (1943). He showed how proximity to the inoculum source of *Rhizoctonia solani* Kuhn affected the intensity of disease. Percentages of damped-off plants were determined each day from 7 to 16 days after radish seeds were planted. Data for regression curves were taken from the 9th day counts from each of two locations (Fig. 15). A slightly different curve was obtained from each of the two sources of inoculum. Different soil types were present at the different locations and may have influenced the rate of seedling mortality. Zero percentage of dead plants was reached at near eight cm. in the Harwood soil type, whereas over 25 percent of the plants were dead at nine cm. in the Allotment soil type. Means of dispersion was by mycelial growth.

Overwintering of the beet downy mildew fungus, *Peronospora schachti*

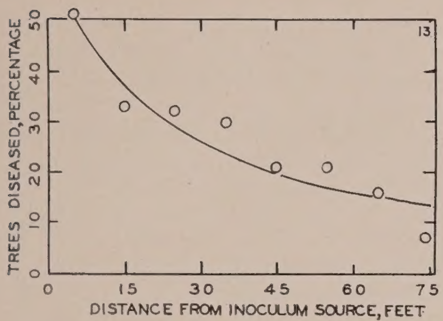

Fig. 13

Incidence of tristeza disease of citrus at distances from a source (data from Bitancourt and Rodriguez).

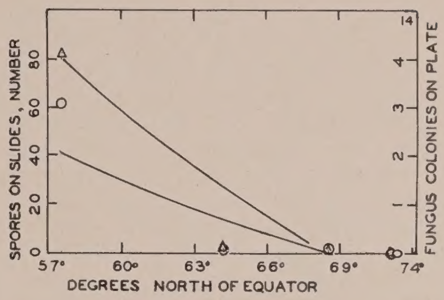

Fig. 14

Incidence of air-borne spores of fungi causing cereal diseases.

Upper curve represents fungus colonies per plate.

Lower curve represents the number of spores caught on vaselined slides (data from Pady, et al.).

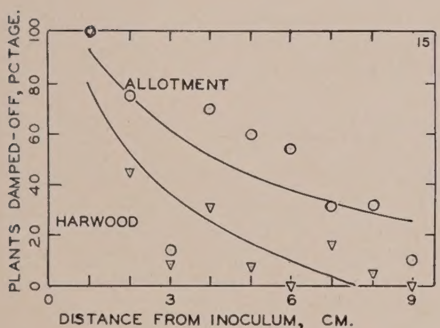

Fig. 15

Incidence of damping-off disease at distances from a source. Curves represent two locations (data from Blair).

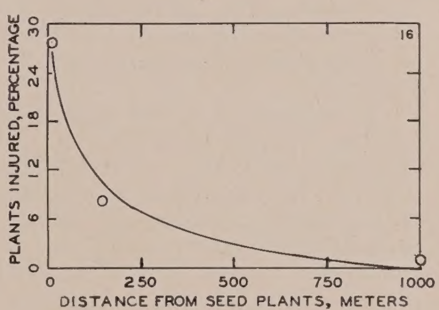

Fig. 16

Incidence of beet downy mildew infections at distances from sugar beet seed plants (data from Höchapfel).

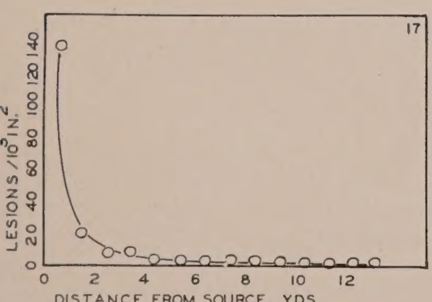

Fig. 17

Number of tobacco blue mold lesions per unit area of field at distances from the source of *Peronospora tabacina* (tracing from Fig. 2, Waggoner and Taylor).

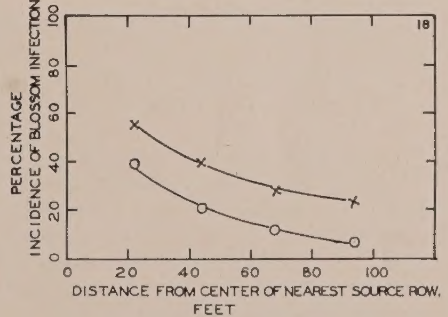

Fig. 18

Incidence of blossom infection by *Sclerotinia laxa* in apricot trees.

Upper curve represents data from 1940.

Lower curve represents data from 1939 (data from Wilson and Baker).

Fckl., which occurs in seed plants of sugar beets was found in initiate primary cycles of the disease. Infections adjacent to seed plants were more frequent than infections at more remote distances from the seed plants according to Hochapfel (1950). From his report the observation "adjacent to" was taken as 10 m., "100–200" was taken as 150 m. and the "1000" gave a third point for which a regression curve was computed (Fig. 16). Over one-fourth of the plants were injured adjacent to the seed plants. Zero percent of the plants was injured, according to the regression curve, at near 1000 m. although one percent was the observation recorded. Dispersion of the spores was by wind.

Fungus spores of *Peronospora tabacina* Adam, causative of tobacco blue mold disease, were found to disperse several yards with the wind and but few yards against the wind. In their report on epiphytotics of tobacco blue mold caused by *P. tabacina*, Waggoner and Taylor (1955) emphasized sanitation by individual growers owing to the short distances spores are dispersed. A reproduction of the gradient shown by these workers is given as Fig. 17. A very rapid decline is shown for the initial part of the regression curve to near four yards from the source. The low incidence at four yards became much lower at 14 yards from the source. No regression formula was given. There is close agreement of observed values with the curve. Means of dispersion is by wind.

In studies on aerial dissemination of spores Wilson and Baker (1946a) reported on the incidence of blossom infection by *Sclerotinia laxa* Ader. and Ruh. A total of seven gradients was obtained in 1939 and 1940 at distances of four apricot trees, 88 feet. Averages from the three gradients obtained in 1939 and from the four gradients obtained in 1940 were used for computing two regression curves (Fig. 18). Percentages of disease were relatively low with each tree row decrease in distance from the spore source, to distances of 88 feet. Similar rates in curvature of the two regression curves show similar rates of disease incidence decrease with distance increase. There was less disease in 1939, however, than in 1940. There is very close agreement of observed and curve values. Conidia of *Sclerotinia laxa* are dispersed by air currents.

Regression rates were determined by the authors according to the formula,

$$y = \frac{A}{xp},$$

". . . where y is the ratio of the percentage of blossom infection in a vertical slice of susceptible tissue (blossom) at a horizontal distance from the source block to the percentage of blossom infection in the source trees, A and p are constants depending on wind velocity and perhaps on other quantities to a lesser extent, and x is the horizontal distance from the center of the nearest source trees." The semi-logarithmic formula was used for computation of the expected numbers used for drawing the regression curves in Fig. 18, since the X^2 (chi-square) values were less than they were from the authors' formula given above. Computation of X^2 was computed by the formula,

$$(O\text{–}C)^2/C,$$

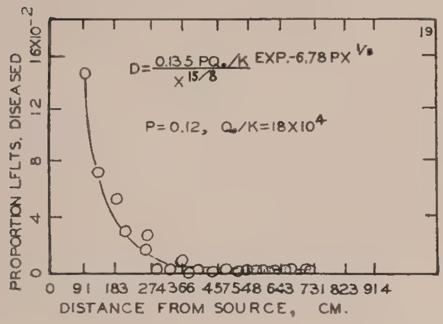

Fig. 19

Incidence of potato late blight diseased leaves at distances from a source of spores (copied from Waggoner).

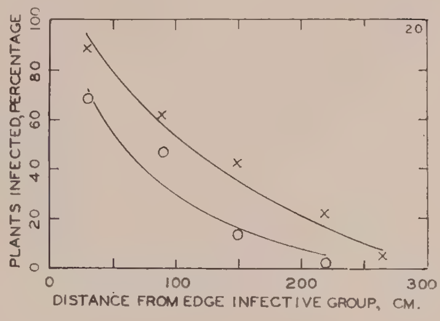

Fig. 20

Incidence of potato late blight disease infections (data from Gregory).

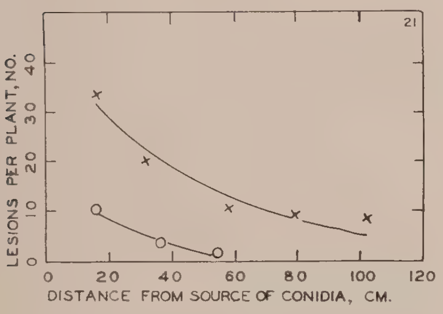

Fig. 21

Incidence of leaf spots on tulip plants at distances from shoot-bearing conidia of *Botrytis tipulae*.

Upper curve represents data from "second bed".

Lower curve represents data from "first bed" (data from Gregory).

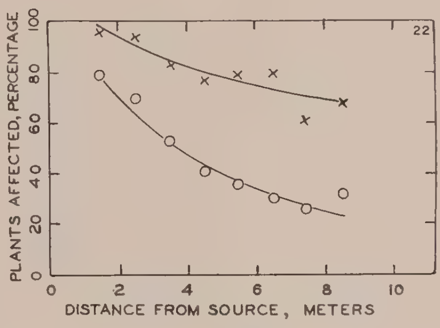

Fig. 22

Spread of powdery mildew from winter to spring barley.

Upper curve represents data from variety *Isaria*, from four directions.

Lower curve represents data from variety *Rimpaus Hanna* from two directions (data from Pape and Rademacher).

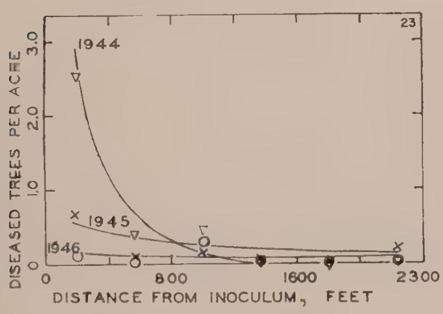

Fig. 23

Annual incidences of trees infected with the Dutch elm disease as related to distances from the source of the fungus spores (data from Liming, et al.).

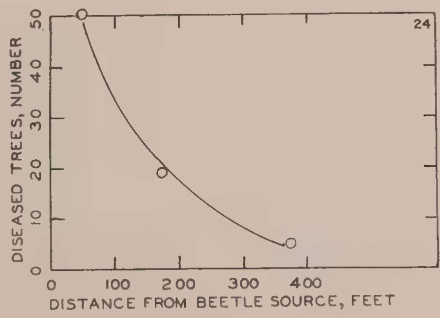

Fig. 24

Incidence of trees infected with the Dutch elm disease associated with distance from the source trees of the native elm bark beetle (data from Parker, et al.).

where "O" is the "observed" value and "C" is the "calculated" value. Total X^2 for the 1939 and 1940 values by the authors' formula gave 8.05 and by the semi-logarithmic formula it was 0.83. Closer agreement of the observed and calculated values was found, therefore, from computations with the semi-logarithmic formula.

Spatial distribution of diseased leaflets was observed by Waggoner (1952) around three isolated sources of the potato late blight disease caused by *Phytophthora infestans* (Montagne) de Bary. Since the observations were presented in graphic form rather than in tabular form the author's Fig. 3 is reproduced to show the rate of incidence (Fig. 19). Very rapid decreases in infections were found to near three meters from the source. Between three and seven meters the gradient of disease showed slight reductions. Primary infections, according to the author, ". . . were limited to an area within 10 meters of the source." Development of the disease was reported as greatest in the direction of air movement during periods favorable for infection. Dispersion is by air currents.

Infected plants serving as foci of spores are generally considered to be the origination of epidemics of late blight disease of potatoes and tomatoes, caused by *Phytophthora infestans* (Mont.) de Bary. Counts of infected plants growing in two locations near primary infections were given by Gregory (1945) (which he abstracted from a report by Limasset [1939]). Two regression curves were drawn from these data (Fig. 20). Low percentages of infections were found at 250 cm. from infected plants. Regression rates were similar for the two locations. Although the semi-logarithmic formula was used to determine the curve slopes, better agreement of observed and curve values might have been obtained if non-transformed data had been used. Means of spore dispersion of the late blight fungus is by wind.

Leaf spots on tulip plants were found related to distances from shoot-bearing conidia of *Botrytis tipulae* (L.) Hopkins according to Wallace (1934) (after Gregory [1954]). Data from two beds were used for drawing regression curves (Fig. 21). Similar rates of disease incidence are shown by the two curves. Low incidences of lesions were reached at comparatively short distances, centimeters from the inoculum source. Rain drop splash was the agent of dispersion although wind may have increased the distance covered by splash droplets.

Spread of powdery mildew, *Erysiphe graminis* D. C., from winter to spring barley was found by Pape and Rademacher (1934) to show effects of distance over a range of meters. Two varieties were under observation and a curve was drawn for each variety (Fig. 22). Incidences of infections were different for the different varieties. The steeper slope of the curve indicated for the variety *Rimpaus Hanna* suggests that a low incidence of disease would be reached at near 15 meters. The lesser slope indicated for the variety *Isaria*, however, suggests that a low incidence of disease for this variety would be reached a great many meters from the spore source. Means of dispersion is by wind.

In a three year study of the Dutch elm disease caused by the fungus *Ceratostomella ulmi* Buisman, Liming et al. (1951) found that most diseased trees occurred within hundreds of feet of the original source.

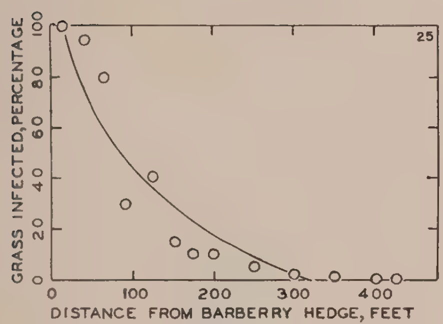

Fig. 25

Incidence of stem rust infections at distances from barberry hedges (data from Johnson and Dickson).

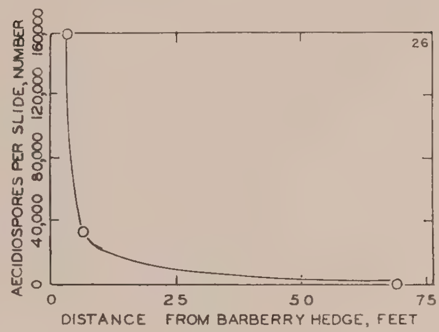

Fig. 26

Aeciospores of wheat stem rust trapped at distances from a barberry hedge (data from Lambert).

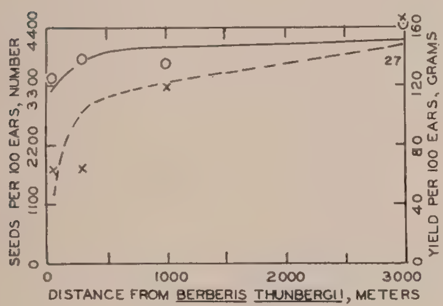

Fig. 27

Incidences of seed count and weight of rye at distances from *Berberis vulgaris* plants.

Scale at left and solid line represent seed count per 100 ears.

Scale at right and broken line represent weight, grams, per 100 ears (data from Fischer).

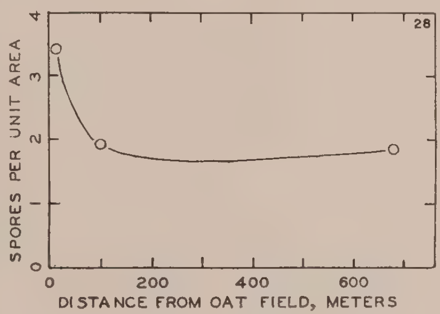

Fig. 28

Uredospores of *Puccinia coronata* trapped at distances from an oat field (data from Gassner).

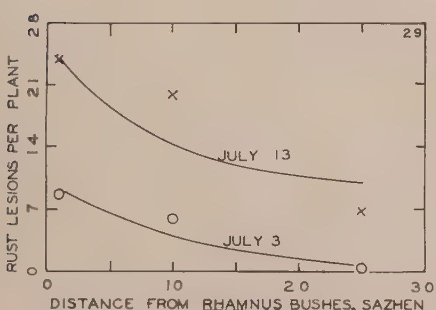

Fig. 29

Incidence of crown rust disease of oats at distances from *Rhamnus* plants (data from Gregory).

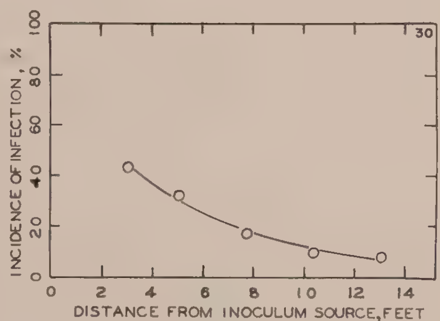

Fig. 30

Incidence of crown rust disease of oats at distances from the spore source (data from Wilson and Baker).

A steady decrease in the incidence of diseased trees around the original inoculum source was observed two and three years after the local outbreak. Three regression curves were drawn to show the results (Figs. 23). Low numbers of diseased trees were reached within 1400 feet of the source. Although there may have been some diseased trees as a result of secondary spread, more diseased trees were found at greater distances the second and third year after the local outbreak. This is evidence of a trend which is discussed under Generalizations. Spread of the fungus causing the Dutch elm disease is by elm bark beetles, *Scolytus multistriatus* Marsh. and *Hylurgopinus rufipes* Eich.

Trees infected with the Dutch elm disease were found associated with the native elm bark beetle, *Hylurgopinus rufipes* Eich., by Parker et al. (1948). More diseased trees were found within 100 feet of beetle infested trees or source of the fungus on each of two years the observations were made (Fig. 24). There was a rapid decline in the number of diseased trees with distance increase from known sources. Low numbers of diseased trees were found 550 feet from the beetle source. There was close agreement of observed and curve values.

Stem rust of wheat, *Puccinia graminis* Pers., infections were most abundant in grass at distances nearest barberry hedges, according to Johnson and Dickson (1919). Low percentages of infections were observed at near 300 feet from the hedge (Fig. 25). Very low percentages of grass infections were observed at distances of 350 to 425 feet from the hedge. Wind was the agent of dispersion of the rust spores.

Aecial spores of stem rust, *Puccinia graminis* Pers., were trapped by Lambert (1929) on 1 x 3 inch glass slides at distances from a barberry hedge. A regression curve was drawn from the data given (Fig. 26). An extremely rapid decrease was found in the spore count to six feet from the hedge. A comparatively low count was made at 69 feet from the spore source. Wind was the agent of dispersion of the rust spores.

An intense outbreak of stem rust, *Puccinia graminis* Pers., on rye plants afforded Fischer (1950) an opportunity to study yield of grain as related to the stem rust. More seed and more weight per head were observed with increasing distances from the rust spore source plants *Berberis thunbergii* D. C. (Fig. 27). Increases in number of seed and weight per head were observed over a 1000 m. range. Slightly different rates of curve slope were found. Although the semi-logarithmic formula was used untransformed data might have been employed to determine the curve slopes. Close agreement of observed and curve values in lacking.

Uredospores of the crown rust of oats, *Puccinia coronata* Corda, were trapped by Gassner (1916) to a maximum distance of 670 meters from the spore source. From the data given a regression curve was drawn (Fig. 28). Forty-five percent as many spores were trapped at 670 as at 5 meters from the source. A very slight reduction was found between 100 and 670 meters. There is close agreement of observed and curve values. Wind was the agent of dispersion.

Incidence of lesions of the crown rust of oats, *Puccinia coronata* Corda. was related by Gregory (1945) to distances from *Rhamnus*

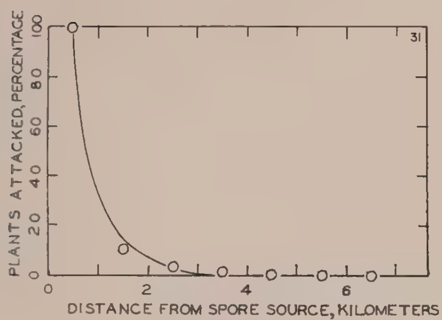

Fig. 31

Incidence of maize rust at distances from a focal point among *Oxalis sticta* plants (data from Zogg).

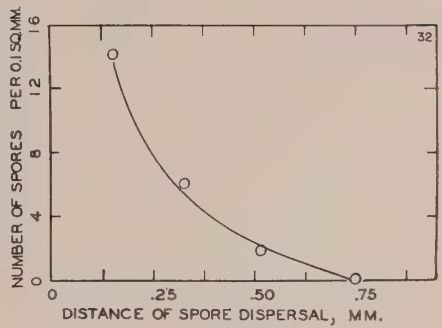

Fig. 32

Dispersion of basidiospores of hollyhock rust (data from Buller).

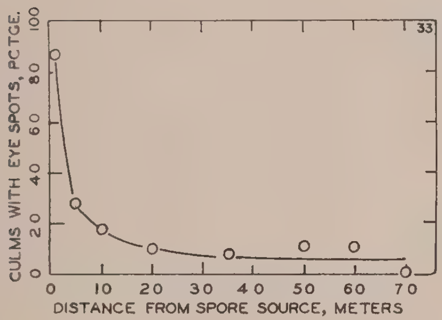

Fig. 33

Incidence of infections of eye-spot disease of wheat (data from Gregory).

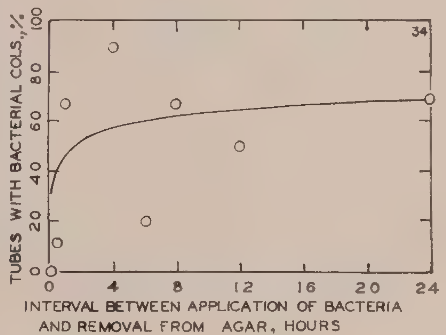

Fig. 34

Frequency of transmission of the crown gall bacterium through sunflower stem segments (data from de Ropp).

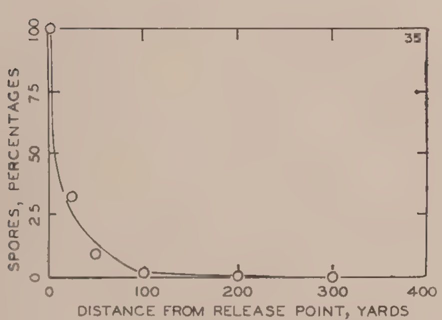

Fig. 35

Lycopodium spore dispersion (data from Hodgson).

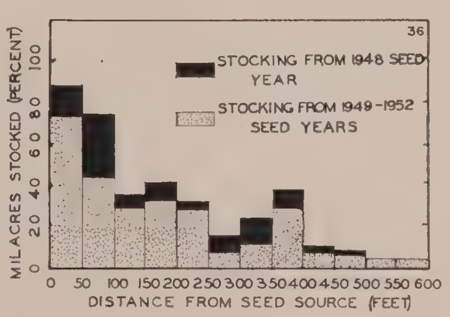

Fig. 36

Natural regeneration of slash pine at distances from the seed source (reproduction of Fig. 7 from Anon.).

bushes in data given by Grushevoi (1929) which I have not seen. Number of lesions per plant for "directly neighboring", were taken as one sazhen distance, and at 10 and 25 sazhen on each of two different count days. A regression curve was drawn to show the results (Fig. 29). The two curves have similar curvilinearity. More lesions per plant were found, however, on the later count, July 13. A straight-line relationship exists with the data although the semi-logarithmic formula was used for illustrating the disease incidence.

Incidence data on the crown rust of oats caused by *Puccinia coronata* Corda were taken by Wilson and Baker (1946b). A well-defined gradient was found by these authors in which the number of lesions per unit of leaf surface decreased with distance increase. Although the authors used the formula discussed on page 10 ($y = \frac{A}{xp}$) the writer employed the semi-logarithmic formula ($E = a + b (\log X)$) for computation of a regression curve (Fig. 30). Gradual decreases in percentages of infection were found from 3 to 13 feet. The regression curve tends to assume a gentle slope at 10–13 feet which might be expected to decrease less rapidly at greater distances. There is close agreement of observed and curve values. Wind was the agent of spore dispersion.

Computation of chi-square values gave 1.37 for the values computed by the formula given by Wilson and Baker (1946a), discussed on page 10. A chi-square value of 2.43 was found for differences between "observed" and "curve" values from the semi-logarithmic formula. Although the chi-square value here shows less agreement with the semi-logarithmic than with the formula given by Wilson and Baker (1946a) the difference is small. Differences were in favor of the semi-logarithmic regression formula, page 2, by very large values.

Maize rust, *Puccinia sorghi* Schw., epidemics were related by Zogg (1949) to *Oxalis sticta* L. plants. Aeciospores from *O. sticta* initiated the disease on maize, *Zea mays* L. in the Rhine Valley. A regression curve was computed from data given (Fig. 31). A very rapid rate of regression was found to have reached a low incidence (nearly zero) at about three kilometers. Wind was the agent of dispersion.

Dispersion of basidiospores of hollyhock rust, *Puccinia malvacearum* Mont., was reported by Buller (1924) to occur within distances of less than one millimeter. This appears to be the shortest range covered by any dispersion study. A regression curve was drawn from the data given (Fig. 32). Approximately 150-fold more spores were taken at 0.15 than at 0.75 mm from the spore source. Dispersion is principally by gravity; aided, perhaps, by ejection.

Influence of distance from spore source of eye-spot of wheat, *Cercosporella herpetrichoides* Fron., was shown by Gregory (1945) from data reported by Oort (1936) which I have not seen. A regression curve was drawn to show the relationship (Fig. 33). A rapid rate of regression was found to about 20 meters from the spore source. Low percentages of culms with eye-spots extended from 20 to 70 meters distance. Fair agreement of observed and curve values exists. Means of dispersion of the spores, according to Gregory (1945), is probably by water.

In order to determine the rate of movement of the crown gall organism, *Agrobacterium tumefaciens* (EFS & Townsend) Conn., bacteria were placed on the cut surfaces of the upper ends of stem fragments of stems of fourweeks old Russian Giant sunflower, *Helianthus annuus* L. Tests were made at intervals to determine infestations at lower ends of the stem fragments. Results of the tests show the rate of movement, Fig. 34, from data given by de Ropp (1948). Percentages of tubes with bacteria increased rapidly, according to the regression curve, for about two hours and after about four hours the rate became much slower. Little increase was indicated after 12–24 hours. There is much scatter of observed values making fit of curve and observed values impossible. Means of dispersion was doubtless by motility of bacteria and gravity.

Dispersal of *Lycopodium* spores was studied by Hodgson (1949). Release of spores was followed by collection of spores at distances from the release site. A regression curve was drawn to show the recovery rate as based on the number of spores recovered at 4 yards taken as 100 percent (Fig. 35). A rapid regression rate extended to 100 yards after which a less rapid rate was found to 300 yards from the release site. There is fair agreement of observed and curve values. Wind was the agent of dispersion.

Spermatophyta

Pinaceae.—Slash pine, *Pinus elliottii* Engelm. was found naturally stocking a drained cypress pond, Anon. (1955). Natural stocking depends on the proximity of seed trees and presumes a favorable growth medium. Drainage of the swamp provided a favorable growth medium for pine. A bar diagram given to show the effects of distance from seed source trees is reproduced as Fig. 36. A low percentage of pine stocking was reached at near 250 feet, and extended to near 600 feet for the 1948 seed year. Stocking in 1948 was shown to have exceeded the four-year stocking, 1949–1952. Wind was the agent of pine seed dispersion.

In a study on the dispersion of pollen grains glass slides were used for sampling the fall. These counts were made within and at different distances from a pine forest of *Pinus echinata* Mill. by Buell (1947). The data are given in terms of percentages, pollen grains falling within the forest were taken as 100 percent. Pollen falling outside the forest was but a fraction of that within; hence, is but a percentage of the within count. Relatively less pollen was counted as distances from the forest margin increased (Fig. 37). Low incidences of pollen counts were made at 0.10, 0.20, and 0.25 mile distances. Less than 20 percent as much pollen fell at 0.10 as within the forest. The greatest rate of reduction was between the forest margin and 0.10 mile distance. Wind was the agent of dispersion.

A very rapid rate of decrease in pollen deposition was found by Wright (1952) for pinyon pine, *Pinus cembroides* (Engelm.) var. *edulis* Voss. A regression curve was drawn from the "total" number of pollen grains collected from the four compass directions. (Fig. 38). Most pollen grains fell within 100 feet of the source tree. The greatest reduction in pollen fall was between 10 and 75 feet. At distances

greater than 100 feet low numbers of pollen grains were found. Wind was the agent of dispersion.

Pollen dispersal from a spruce tree, *Picea abies* Karst., was found by Wright (1952) to be restricted to comparatively short distances. Although vaseline coated slides were placed at distances to one mile from the source tree, the pollen frequencies were so low that only those slides within 330 feet were counted (Fig. 39). Zero pollen collection was reached at near 325 feet from the source, according to the curve. This compares with 9.6 pollen grains at the source, and suggests that pollen from this tree has wide-spread dispersion. Observed and curve values lack close agreement. Wind was the agent of dispersion.

Pollen grains were collected by Wright (1952) at various distances from an Atlas cedar tree, *Cedrus atlantica* Manetti var. *glauca* Carr. Data were combined from the 1946–1947 collections for calculation of a regression curve (Fig. 40). Curve values of 189.0 and 0.1 pollen grains were calculated for deposition at 40 and 700 feet, respectively, from the source tree. Wind was the agent of dispersion.

Pollen grains were collected by Wright (1952) at various distances from a Lebanon cedar tree, *Cedrus libani* Loud. A regression curve was drawn from the data given (Fig. 41). Counts of pollen grains to 195 feet from the source tree showed a gradual decrease. Expected numbers of pollen grains at 15 and 195 feet were 128 and 22, respectively. Close agreement of observed and curve values is lacking. Wind was the agent of dispersion.

Poaceae.—Pollen grains of cocksfoot, *Dactylus glomerata* L., were found by Jensen and Bøgh (1941) to have dispersed hundreds of meters distance. Three regression curves were drawn from the three sets of data given (Fig. 42). Similar rates of dispersion are illustrated by the three curves. The curve in the highest position represents dispersion provided by a strong wind, the middle curve represents dispersion provided by a weak wind and the curve in the lowest position represents dispersion provided by a wind of three meters per second. Wind was the agent of dispersion.

Pollen shedding of bromegrass, *Bromus inermis* Leyas, occurs in the late afternoon at temperatures above 70° F., and during westerly, southerly, or easterly winds; according to Jones and Newell (1946). A regression curve was drawn to show the rate of pollen dispersion (Fig. 43). Approximately one percent as much pollen fell at 60 rods from as in the center of the pollen source. The distance at which zero pollen fall could be expected, however, was at some distance in excess of 60 rods. There is close agreement of observed and curve values. Wind was the agent of dispersion.

In ecological studies on *Bromus tectorum* L. and other annual bromegrasses, Hulbert (1955) trapped seeds at distances from seed producing plants. A regression curve was drawn to show the rate of dispersion of *B. tectorum* (Fig. 44). Most seeds were taken within one meter of the seed source. Zero, 1 and 4 seeds were taken at 1, 2.5, and 5 meters, respectively from the origin. The regression curve shows a low rate of seed fall occurred within four meters and remained low. There is much scatter of observed values making it impossible to define the regression curve. Wind was the agent of dispersion.

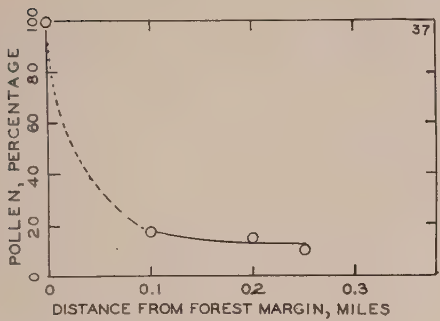

Fig. 37

Dispersion of shortleaf pine pollen from source trees (data from Buell).

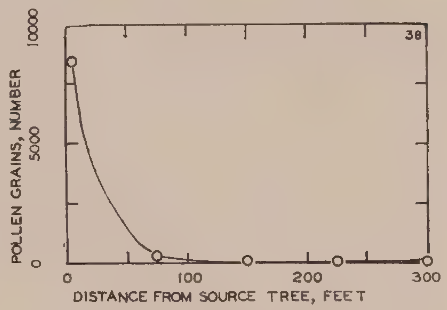

Fig. 38

Dispersion of pinyon pine pollen from a source tree (data from Wright).

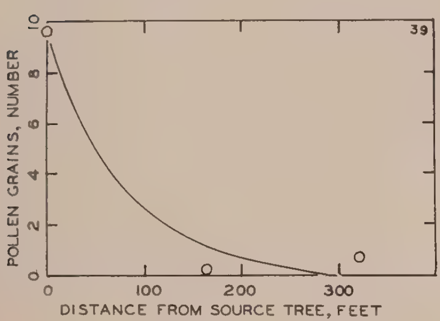

Fig. 39

Dispersion of spruce pollen from a source tree (data from Wright).

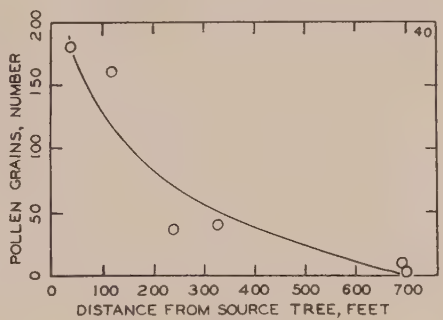

Fig. 40

Dispersion of Atlas cedar pollen from a source tree (data from Wright).

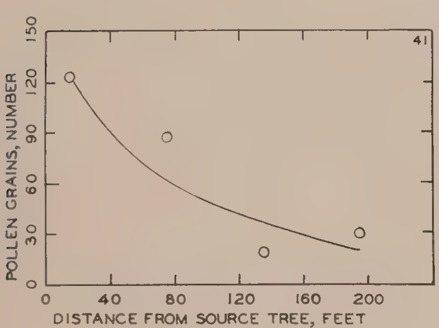

Fig. 41

Dispersion of Lebanon cedar pollen (data from Wright).

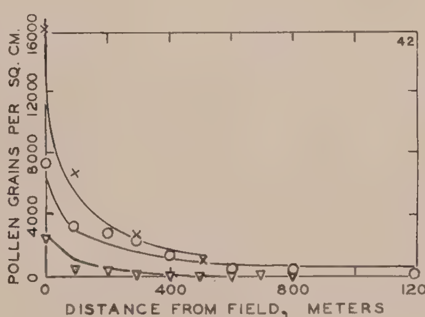

Fig. 42

Dispersion of cocksfoot pollen.

Upper curve represents data from 1939, strong wind.

Middle curve represents data from 1939, weak wind.

Lower curve represents data from 1940 (data from Jensen and Bøgh).

Albino seedlings in Pensacola Bahia grass, *Paspalum notatum* Flugge, showed the amount of outcrossing from isolation blocks in studies by Hodgson (1949). This grass is self sterile and is "highly cross-pollinated" according to Hodgson (1949). Two regression curves were drawn, one for heads exposed June 12–July 5, the other for heads exposed July 7–August 4 (Fig. 45). Although the slopes of the two curves are very similar, the curve representing outcrossing in the early part of the season had 9.2 percent more crossing than the latter part of the season which had 12.1 percent more outcrossing at 15 rods than at O distance from the isolation block. Differences between the curves are between 2 and 4 percent over the distance range, which may be attributed to seasonal effects.

Pearl millett, *Pennisetum glaucum* (L.) R. Br., pollen was found to disperse to distances of 400 yards downwind from the release site, Hodgson (1949). A regression curve was drawn to show the rate of percentage decrease (Fig. 46). A rapid decrease was found to near 50 yards. The rate became less rapid from near 50 to less than 300 yards from the release site where zero was reached, according to the regression curve. Wind was the agent of dispersion.

Pollen of ryegrass, *Lolium* sp., dispersed to distances of several hundreds of meters according to Jensen and Bøgh (1941). Considerable data were taken at different wind velocities and over the years 1939 and 1940. These data are summarized by five regression curves (Fig. 47) and by a generalized curve (Fig. 48). The curves in the highest and lowest positions represent pollen dispersed by very strong winds. Low incidences of pollen were found at 800 meters by the five curves and also by the generalized curve. There is fair agreement of observed and curve values. Wind was the agent of dispersion.

Pollination of perennial ryegrass, *Lolium perenne* L., was studied by Wit (1952) in plantings of smooth clones at distances from rough clones. Distance effects through cross-pollination were rather marked in changing smooth to rough clonal characters (Fig. 49). Low percentages of cross pollination were reached at near 300 centimeters from rough clonal plants. There is close agreement of observed and curve values. Wind was the agent of pollination.

Dispersal studies of crested wheatgrass, *Agropyron cristatum* (L.) Gaertn., were reported by Jones and Newell (1946) for a two-year period. Data from the two-year averages were taken for computing constants and drawing a regression curve (Fig. 50). Based on the number of pollen grains taken in the center of the source field as 100 percent the percentages at 5, 15, and 25 rods from the field were 21.0, 8.5, and 2.9, respectively. Although a rapid rate of pollen reduction with distance increase is indicated, there would be considerable cross pollination within 25 rods from the source field. There is a close agreement of observed and curve values. Wind was the agent of dispersion.

Intermediate wheatgrass pollen, *Agropyron intermedium* (Horst) Beauv., dispersion data were collected by Jones and Newell (1946) over a two-year period. A regression curve was drawn from the averages of the pollen grains collected over the period of observation (Fig. 51). Observed pollen grain counts averaged 45 grains at five rods,

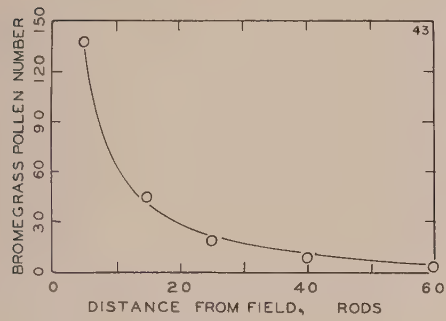

Fig. 43

Dispersion of bromegrass pollen (data from Jones and Newell).

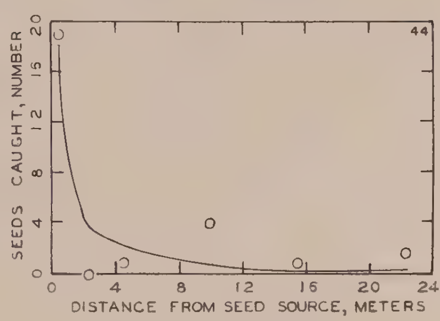

Fig. 44

Dispersion of annual bromegrass pollen (data from Hulbert).

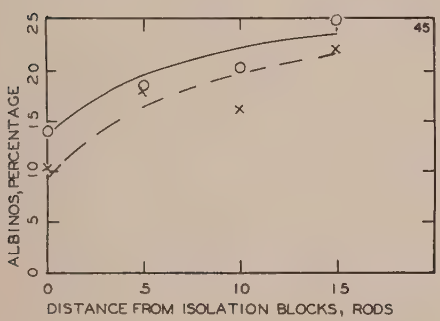

Fig. 45

Incidence of albino seedling Pensacola Bahia grass.

Upper curve represents data from heads exposed June 12-July 5.

Lower curve represents data from heads exposed July 7-August 4 (data from Hodgson).

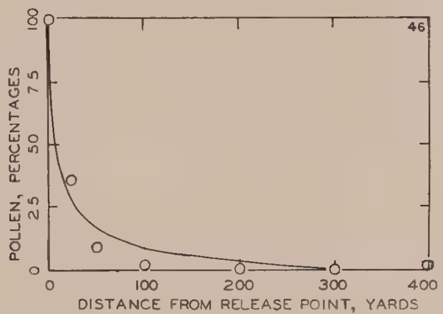

Fig. 46

Dispersion of pearl millett pollen (data from Hodgson).

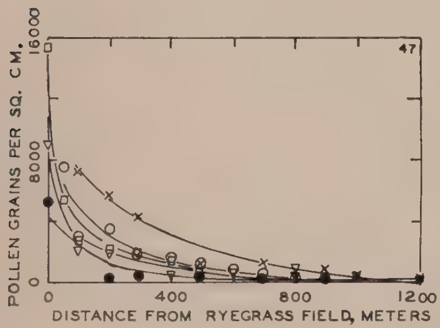

Fig. 47

Dispersion of ryegrass pollen.

Different curves represent data from different wind speeds (data from Jensen and Bøgh).

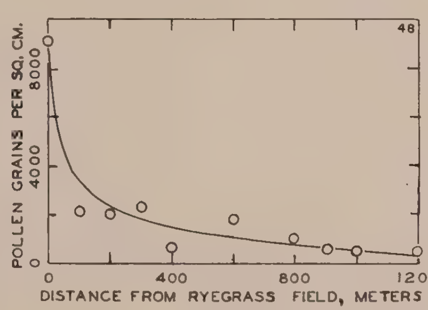

Fig. 48

Dispersion of ryegrass pollen (data from Jensen and Bøgh).

13 grains at 15, and seven grains at 25 rods from the field. Wind was the agent of dispersion.

Data on rye, *Secale cereale* L., pollen dispersion were given by Jensen and Bøgh (1941). These data showed regular decreases in numbers of pollen grains with increase in distance (Fig. 52) from the source. Approximately 10 percent as many grains of pollen were found at 700 as at O meters from the source. Rye pollen is dispersed much further than the 700 meter maximum distance observed, according to the regression curve. Wind was the agent of dispersion.

Data on rye, *Secale cereale* L., pollen dispersion in the northern direction were given by Jones and Newell (1946). Sixty rods was the maximum distance of observations, but a regression curve was drawn to show the results (Fig. 53). Approximately two and one-half percent as many pollen grains were taken at 60 as at five rods distance from the pollen source. Wind was the agent of dispersion.

Pollen grains from timothy, *Phleum pratense* L., dispersed several hundreds of meters, according to Jensen and Bøgh (1941). Three regression curves were drawn from the data given (Fig. 54). Curves having similar rates of slope were found for the different wind speeds, 1.9, 3.5, and 4.0 meters per second. Low counts of pollen grains were reported for the three sets of observations. Wind was the agent of dispersion.

Rice, *Oriza sativa* L., pollen dispersion was studied by Rodrigo (1925) in connection with pollination and flowering of the plants. From the averages of 16 observations at each distance point a regression curve was drawn (Fig. 55). Most pollen grains fell within 200 centimeters of the source in a rapid rate of regression from 25 centimeters. There was excellent agreement of observed and curve values. Although dehiscence was a means of dispersion and may have been of some importance, wind was considered of more importance in the dispersion of rice pollen.

Switchgrass, *Panicum virgatum* L., pollen dispersal was studied in 1944 and 1945 by Jones and Newell (1946). Pollen dispersal was determined by the number of pollen grains which fell on 16 mm glass slides at distances from the field. A regression curve was drawn to illustrate the results of both years (Fig. 56). Low counts of switchgrass pollen were made as compared with counts from some other species, cocksfoot and ryegrass for example. Twenty seven grains were found at five rods and one grain was found at 60 rods from the source. There is very good agreement of observed and curve values. Wind was the agent of dispersion.

Considerably more work has been done on pollination of corn, *Zea mays* L., than with any other species of the grass family. Needs for purity of seed have demanded more knowledge of corn pollen dispersal than of other species. Wind is the chief agent of pollination.

Rather wide-spread dispersion of corn pollen is suggested by the work of Jones and Newell (1946). A regression curve drawn from the data given by them is presented in Fig. 57. Almost five percent as much pollen was taken at 60 as at five rods from the field margin. There is fair agreement of observed and curve values.

Studies by Bateman (1947b) on contamination among corn varieties

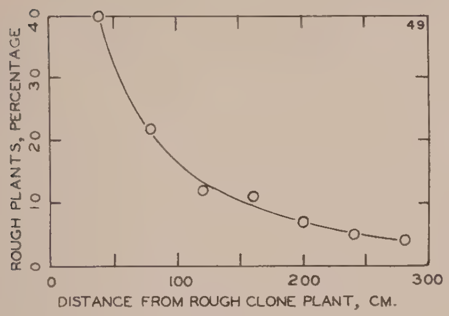

Fig. 49

Incidence of perennial ryegrass contamination (data from Wit).

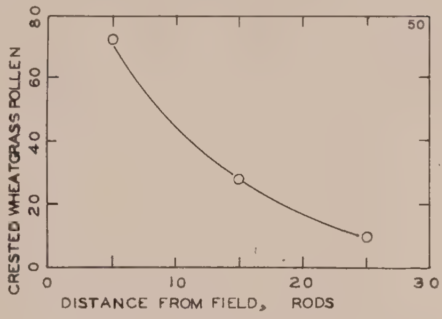

Fig. 50

Dispersion of crested wheatgrass pollen (data from Jones and Newell).

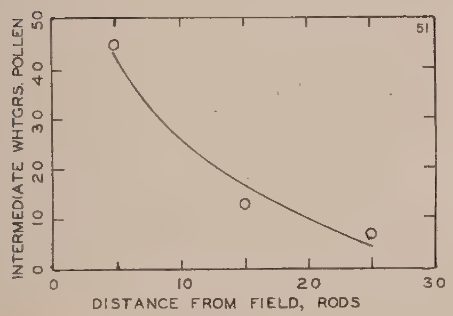

Fig. 51

Dispersion of intermediate wheatgrass pollen (data from Jones and Newell).

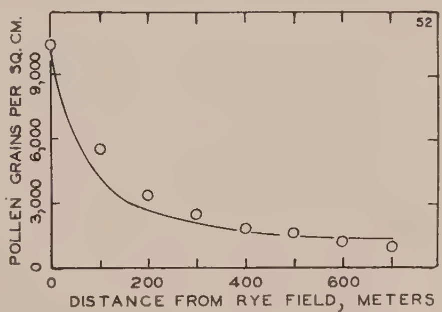

Fig. 52

Dispersion of rye pollen (data from Jensen and Bøgh).

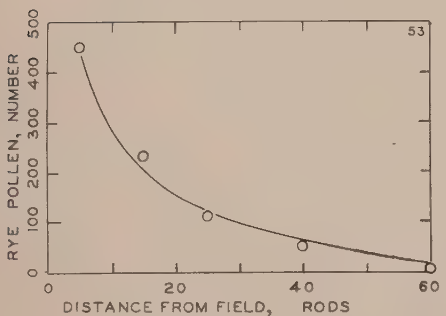

Fig. 53

Dispersion of rye pollen (data from Jones and Newell).

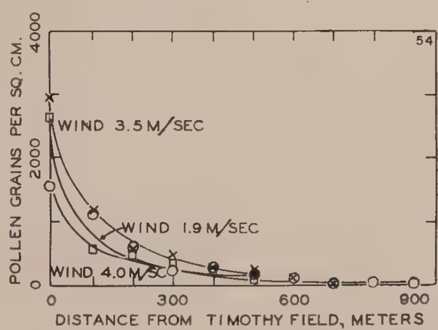

Fig. 54

Dispersion of timothy pollen (data from Jensen and Bøgh).

showed variations in tasseling and silking. In order to eliminate these factors as sources of error, he measured pollen dispersal as related to distance from the source. A curve was drawn among the observed values as in Fig. 58.

Studies of corn pollen dispersal by Hodgson (1949) were made by releasing the pollen grains and sampling the deposition down-wind from the release point. A regression curve was drawn to show the results (Fig. 59). A low percentage (3.0) was observed at 50 and no pollen was found 100 yards from the release point. The regression curve reached zero at near 65 yards from the release point. Close agreement of observed and curve values was lacking.

Cross pollination of corn seed was reduced by 60 feet of distance according to Bateman (1947b). A regression curve was drawn to show the generalized trend (Fig. 60). Zero hybridization was reached at near 70 feet by the curve. There is lack of consistency of observed and curve values.

Seed-settings of corn at various distances from a pollen source were shown by the studies of Haskell and Dow (1951). Seed-setting bore no relationship to direction from pollen source. Results of seed-set on all eight stringers were, therefore, pooled to obtain averages for each distance class. A regression curve was drawn from these averages (Fig. 61). Reduction in seed-set was found to be more than 40 feet from the pollen source, the maximum distance covered by the data. Zero seed-set was at some distance greater than 40 feet. There is fair agreement of observed and curve values. A regression curve by Haskell and Dow (1951, Fig. 2) was derived by conversion of seed-set, the dependent variable, to logarithms. Results of plotting showed that about the same degree of agreement existed whether the distance or the seed-set were transformed to logarithms. A regression curve derived from non-transformed values would doubtless have shown closer alignment than either of the above mentioned transformations.

A study in natural crossing of blue on yellow corn was reported by Jones and Brooks (1950) from data given by Meijers (1937) which I did not see. A regression curve was drawn from the data given (Fig. 62). A low percentage (seven) of outcrossing at one rod from the pollen source became lower ($\frac{6}{10}$ of 1 percent) at two rods and was lower at three and four rods. There was fair agreement of observed and curve values.

A field of silking white corn was the reception medium of pollen from a field of yellow corn on the windward side. Contamination was determined by obtaining the percentage of yellow kernals that occurred at various distances from the yellow corn. Data from this study by Jones and Brooks (1950) from the work of Salmanov (1940) which I did not see, was used for drawing a regression curve (Fig. 63). A low percentage (0.33) was reached at 10 rods from the source of the contaminant pollen. The windward side of the receptor medium and the white corn variety may explain the low percentages at distances greater than 10 rods. Fractional percentages were found, however, to distances of 140 rods from the foreign pollen.

Results of three seasons experiments were given by Jones and Brooks (1950) as percentages of outcrossed grain at eight distances of

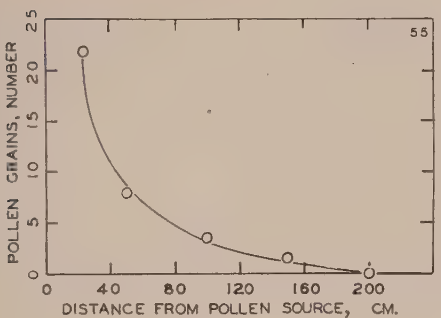

Fig. 55
Dispersion of rice pollen (data from Rodrigo).

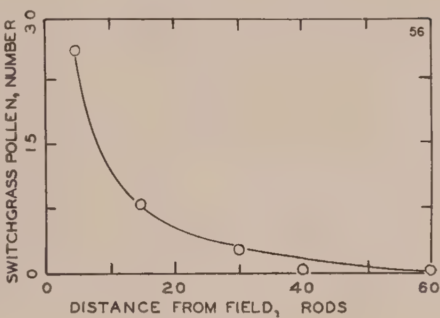

Fig. 56
Dispersion of switchgrass pollen (data from Jones and Newell).

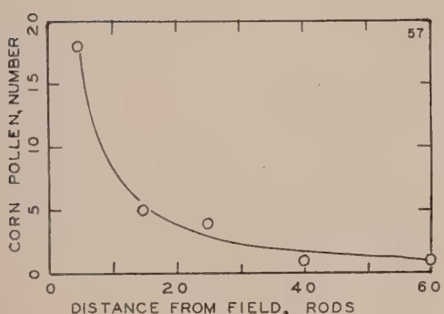

Fig. 57
Dispersion of corn pollen (data from Jones and Newell).

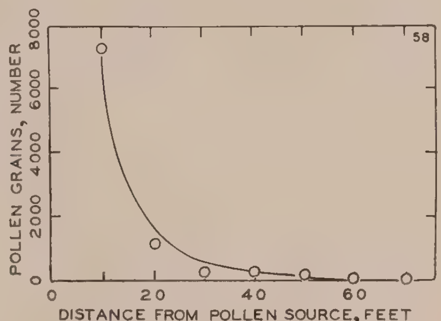

Fig. 58
Dispersion of corn pollen (data from Bateman).

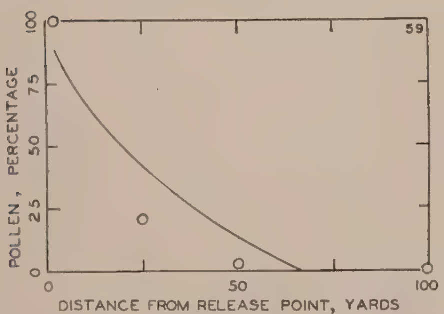

Fig. 59
Dispersion of corn pollen (data from Hodgson).

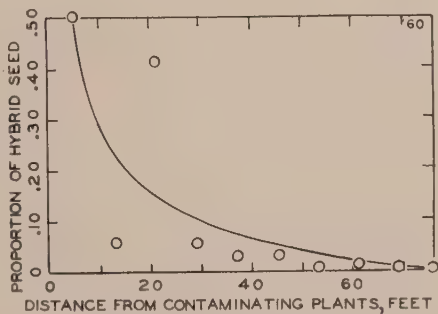

Fig. 60
Contamination of corn by foreign pollen (data from Bateman).

isolation. Blocks of Honey Jane corn were planted to act as receptors to foreign pollen at distances from other corn plants. A field of Yellow Surcropper corn was planted to provide the foreign pollen. Regression curves were drawn to show the results (Fig. 64). Low percentages of outcrossed seed were found at 60 rods from the foreign pollen source. Rainy weather, low wind velocities and other factors were different in different years and caused different rates of regression. Regardless of factors involved only a fraction of one percent outcrossing was observed each year at 60 rods from the foreign pollen.

Salicaceae.—Poplar, ***Populus nigra*** var. *italica* Du Roi, pollen dispersion data were taken by Wright (1952). These data, taken on one day, were used for the determination of a regression curve (Fig. 65). A very gentle sloping curve resulted from the regression calculations. Lack of agreement of curve and observed values suggests that further studies are needed to determine a more definite rate of regression of this species. Wind was the agent of dispersion.

Counts of pollen grains from eastern cottonwood trees, ***Populus deltoides*** Bartr., were made by Wright (1952) for each of four days during the time a tree was in bloom. A regression curve was drawn to show the expected pollen dispersion to 3550 feet from the source tree (Fig. 66). A low of 0.3 grain at 3550 feet compares with 115.0 grains at 25 feet from the pollen source, according to the regression curve. Observed values are scattered making them agree poorly with the curve values. Wind was the agent of dispersion.

Ulmaceae.—Results of pollen deposited at distances from an American elm, ***Ulmus americana*** L., were obtained by Wright (1952). Distances to 5500 feet were used for computing a regression curve (Fig. 67). A zero pollen grain figure was reached at near 3500 feet by the regression curve. Since slightly less than 500 grains was computed for zero distance, the distance range for elm pollen is suggested by these data. Wind was the agent of dispersion.

Chenopodiaceae.—A source of contaminant pollen in a planting of Crimson Ball beet, ***Beta vulgaris*** L., was used by Bateman (1947b) to study distance effects on hybridization. The Spinach beet variety was planted in arms to the north and to the south of the contaminant source. Although this is a wind-pollinated crop plant, there was no apparent difference in contamination of the plants in the different directions. The data obtained from the two arms were, therefore, pooled for use in determining the regression curve (Fig. 68). A very rapid decrease was found in the percentage of hybridization to near 20 feet. Small amounts of contamination were found to 70 feet from the source of the contaminant pollen. There is close agreement of observed and curve values.

Sugar beet, ***Beta vulgaris*** L., pollen was found by Jensen and Bøgh (1941) to disperse to distances of several hundred meters (Fig. 69). A rapid rate of pollen reduction to 200 meters was followed by a slower rate of reduction to 800 meters from the source. Zero pollen was reached, however, at some distance in excess of 800 meters. There is close agreement of observed and curve values.

Cruciferae.—A test was made by Bateman (1947a) to determine any effect of row masses on contamination of turnip, ***Brassica rapa*** L.

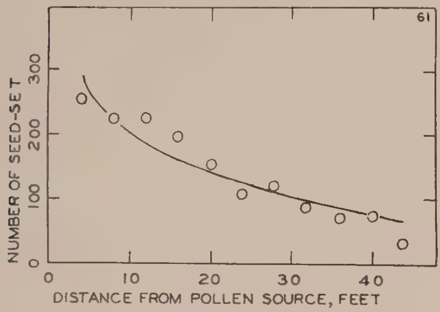

Fig. 61

Seed setting at distances from the pollen source (data from Haskell and Dow).

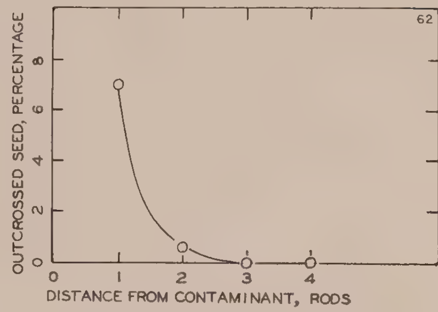

Fig. 62

Incidence of crossing of yellow corn at distances from blue corn (data from Jones and Brooks).

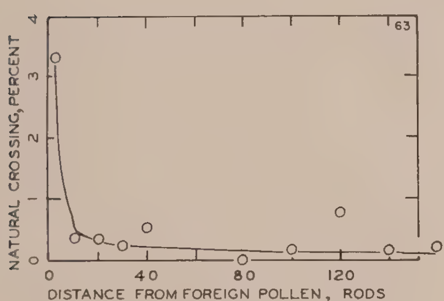

Fig. 63

Natural outcrossing in corn (data from Jones and Brooks).

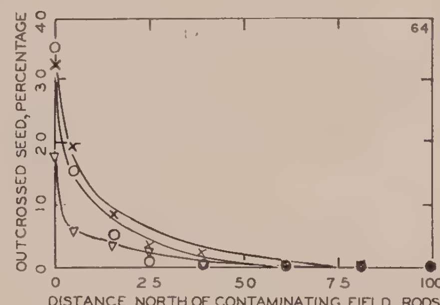

Fig. 64

Outcrossing in corn
Upper curve represents data from 1949.
Middle curve represents data from 1947.
Lower curve represents data from 1948 (data from Jones and Brooks).

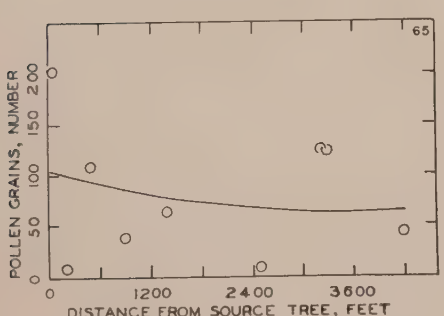

Fig. 65

Dispersion of poplar pollen (data from Wright).

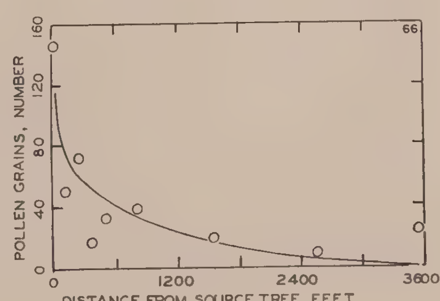

Fig. 66

Dispersion of Eastern cottonwood pollen from a source tree (data from Wright).

One, three, six, and 12 rows were the masses of Scarlet Globe variety used. These rows were planted at right angles to a plot of the contaminant variety, Icicle, so that distance effects were also determined; these are shown in Fig. 70. Decreased proportions of hybrid seed were found with increased distances from the contaminant source in all row masses. Low proportions were found within 40 feet of the contaminant. Larger numbers of plants of the receptive variety reduced the proportions of hybrid seed. Fewer hybrids were found at given distances in the 12-row mass than in the six-, three-, or the one-row mass. Further reference is made to this subject under Generalizations. Insects were important agents of dispersion of turnip pollen.

Contamination of Scarlet Globe radish, *Raphanus sativa* L., by pollen of the Icicle variety was found by Bateman (1947a) to reach low levels at six feet from the contaminant source. Rather intensive studies were made to determine density of planting on spread of the contaminant. Regression curves were drawn to show the incidences of contamination from the various data (Fig. 71). At six feet from the Icicle variety contamination was low in all curves. Zero contamination, however, was at some distance in excess of six feet. Fair agreement of observed and curve values exists and gives one confidence in the data. Insects are important agents of dispersion.

Rosaceae.—Observations were recorded by Richey (1946) on the distribution of apple, *Malus pumila* L. pollen by wind. Glass slides were exposed for 24-hour periods at different distances from the tree source. A regression curve was drawn from the data given for slides exposed at six inches above the ground (Fig. 72). In the distance covered, 12 to 30 feet, there was a reduction in the pollen fall of about one-fifth. An interesting extrapolation, to the one-foot distance, suggests that between 1 and 30 feet the pollen fall was reduced about one-half.

In studying the set of apples, *Malus pumila* L. Roberts (1945 and correspondence) reported that several factors influenced pollination. Data were given, however, showing the distance from a pollen source to which honeybees were effective pollinators of the Delicious variety. A regression curve was drawn to show the relationship (Fig. 73). The set of fruit was reduced by about one-half in the thirty-five feet between 7 and 42 feet. Although a relationship exists between fruit set and the distance from the pollen source there are other factors of much importance in fruit set. Blossom structure, honeybee populations, insects other than honeybee, weather during the bloom period and other varieties are all important factors in securing satisfactory apple crops.

Data on apple, *Malus pumila* L., were obtained by Wright (1952) on the number of pollen grains deposited at 0, 165, and 330 feet from the pollen source. Figure 74 is given to show the relationship of distance and pollen grains counted. According to the regression curve 13.1 and 0.9 grains could be expected at 0 and 330 feet, respectively, from the source. Close agreement of observed and curve values is lacking. Wind was the agent of dispersion.

Leguminosae.—Much has been said and written of increased legume seed yields from visits of the bloom by honeybees. Yields of alsike

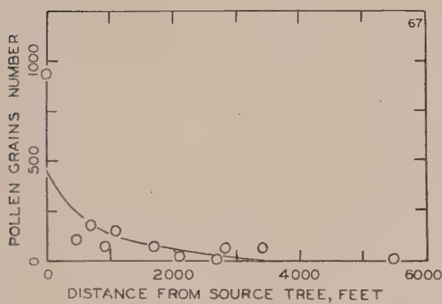

Fig. 67

Dispersion of elm pollen from a source tree (data from Wright).

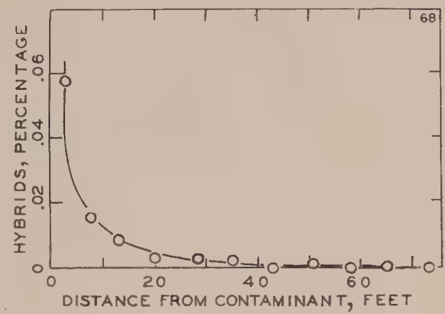

Fig. 68

Incidence of contamination of beet (data from Bateman).

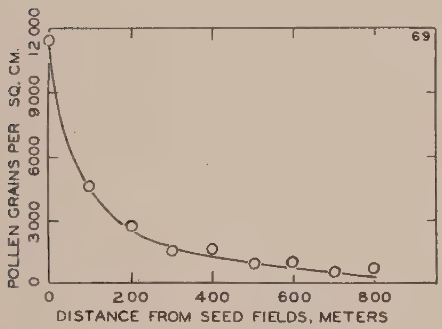

Fig. 69

Dispersion of beet pollen (data from Jensen and Bøgh).

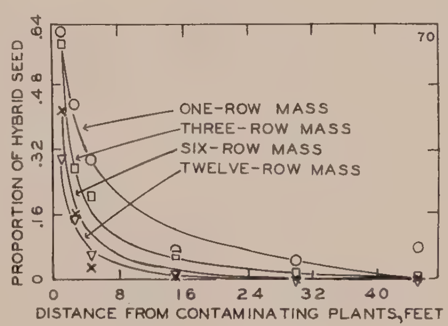

Fig. 70

Incidence of turnip contamination. Different curves represent data from different row-masses (data from Bateman).

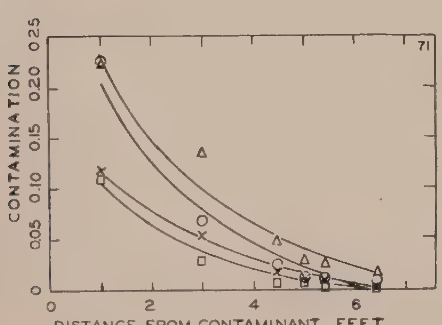

Fig. 71

Incidence of contamination of radish. Different curves represent different blocks (data from Bateman).

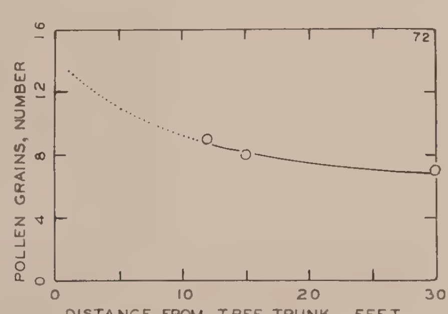

Fig. 72

Dispersion of apple pollen by wind (data from Richey).

clover, *Trifolium hybridum* L., seed were found by Harrison et al. (1945) to be greater nearest apiaries than at more remote distances. Two regression curves were drawn from the given data (Fig. 75). Alsike clover yields were reduced very perceptibly at two miles from the apiaries. The regression curve drawn from the 1944 data has more slope than the curve from the 1943 data. The ¼ mile or less distance observation made in 1944 appears to be shown by yields that are too small. Insects were the principal agent of dispersion.

White clover, *Trifolium repens* L., seed yield was influenced by distance from an apiary according to Harrison et al. (1945). Yield data were given from each of three distance points from which a regression curve was drawn (Fig. 76). At distances to one mile from the apiary the increases in seed yield were more marked than the increases at greater distances. There is very close agreement of observed and curve values. Insects were the agents of dispersion.

Production of red clover, *Trifolium pratense* L., seed was reported by MacVicar et al. (1952) in which more seed was produced near the apiary compared with the yield 1400 yards away (Fig. 77). Slight increases in seed yield were found for the distance range covered by the observations to 1400 yards. Close agreement of observed and curve values is lacking. Insects were the agents of dispersion.

Red clover, *Trifolium pratense* L., seed production was considerably increased nearer honeybee colonies over yield at more remote distances (Anon., 1953). Results were given for two years of observations from which a regression curve was drawn (Fig. 78). Yields of seed were considerably less at 1200 than at 400 feet from the colonies.

Tests on natural hybridization of lima beans, *Phaseolus lunatus* L., were conducted by Allard (1954). The luteus strain L124 was planted at distances from beans having normal chlorophyll. Data were given for each of two years to distances of 32.5 feet from contaminant pollen. Two regression curves were drawn, one for each year (Fig. 79). Rapid reductions in hybridization were found with distance increase to near 12 feet. From 12.0 to 32.5 feet there was very little reduction in hybridization. There is similarity in position and in curvature of the two regression curves. Excellent agreement of observed and curve values exists. Insects are agents of pollination.

Malvaceae.—Natural crossing of cotton in the western Punjab was most frequent at 12.5 feet from the marker plants according to Afzal and Khan (1950). Crossing decreased with distance increase from either local or American varieties (Fig. 80). At 60 feet from the contaminating pollen source crossing had decreased to a low degree. All regression curves had reached 0.00 within 70 feet. Natural crossing was found to have differed considerably with pickings, according to Afzal and Khan (1950). Contamination decreased so much toward the last picking that there was slight chance of encountering hybrids in the final harvest. This was related to different periods of flowering. Foreign pollen was less effective in pollinating the flowers than self-pollen. Hence, self pollination alone is more important than cross pollination with increase in distance from the contaminant. Another observation reported by the authors was that natural crossing occurred about equally in all directions.

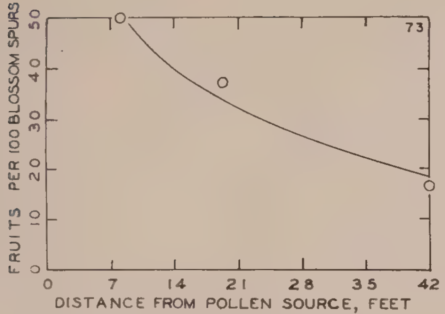

Fig. 73

Incidence of fruit set at distances from the pollen source (data from Roberts).

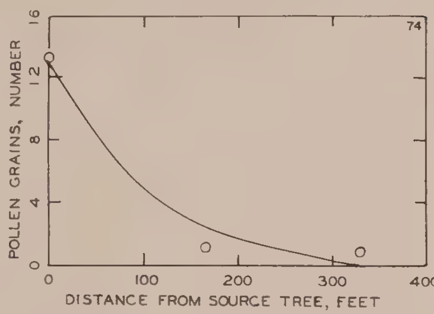

Fig. 74

Dispersion of apple pollen from a source tree (data from Wright).

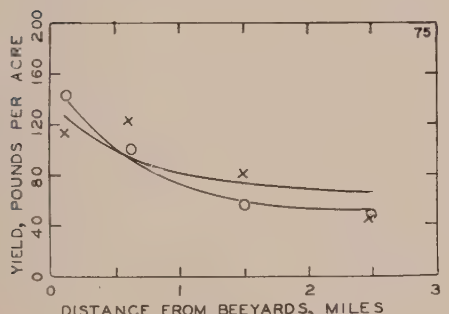

Fig. 75

Incidence of alsike clover seed yields at distances from an apiary.

Circles represent data taken in 1943.

X characters represent data taken in 1944 (data from Harrison, et al.).

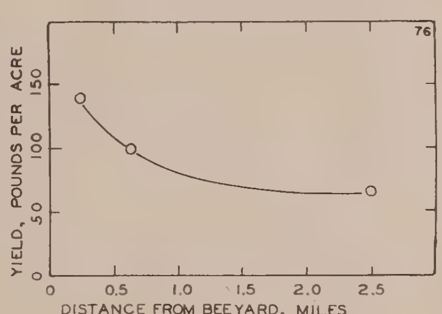

Fig. 76

Incidence of white clover seed yields at distances from an apirary (data from Harrison, et al.).

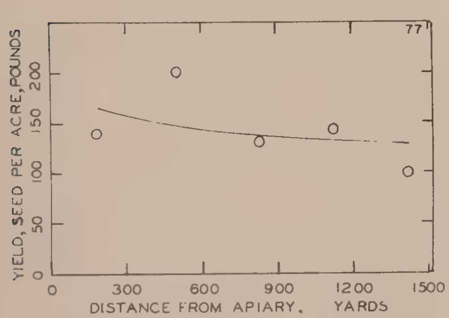

Fig. 77

Incidence of red clover seed production at distances from an apiary (data from MacVicar, et al.).

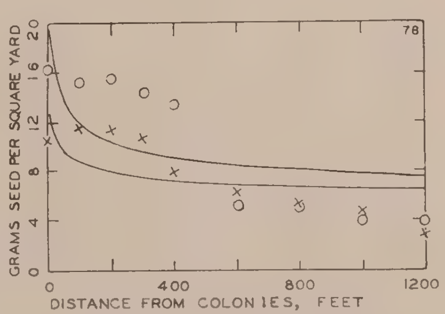

Fig. 78

Incidence of red clover seed production at distances from an apiary.

Upper curve represents data taken in 1950.

Lower curve represents data taken in 1951 (data from Anon.).

Natural crossing of cotton was studied by Balls et al. (1929) in Egypt. A regression curve was drawn from the data given (Fig. 81). The rate of crossing reached zero at near 90 meters from the contaminant, according to the regression curve. Owing to poor agreement of observed and curve values, however, more data are desirable.

The extent of natural crossing of cotton in Oklahoma was studied by Green and Jones (1953). They found variations between areas where cotton was grown and reported that these variations, ". . . may be presumed to reflect differences in insect populations and abundance of cotton in the area." They planted De Ridder cotton as the contaminant source and blocks of green cotton about the contaminant to study isolation requirements. Regression curves were drawn from data taken in blocks grown at different distances from the contaminant source (Fig. 82). Most hybridization occurred within 50 feet of the contaminant source. Blocks at successively greater distances showed successively less contamination. Low percentages of crossing were found at 175–200 feet.

Three classes of seed were recognized by Green and Jones (1953) as follows: Breeders, Registered and Certified. Greater isolation distance is required for Breeders than for Registered, and for Registered than for Certified seed. Hence, the purpose or objective sought for the seed may determine the degree of isolation required. Further reference is made to the subject under Generalizations.

In order to study visitation of cotton flowers by bumble bees, *Bombus* sp., a single Asiatic cotton, *Gossypium arboreum* L., flower and a single upland cotton, *G. hirsutum* L., flowers were dusted with methylene blue dye. Later 40 Asiatic and 26 Upland nearby cotton flowers were examined for dye particles. The dye particles were presumed to have been distributed by the bumble bees. Two curves were drawn from the data given by Stephens and Finker (1953) (Fig. 83). Two curves having similar rates of slope with distance increase are shown. A greater percentage of blossoms with dye particles was found on Upland than on Asiatic cotton blossoms. This suggests more visitations on Upland than on Asiatic flowers. Although the semi-logarithmic formula was used to determine the curve slope and position untransformed data might have given closer agreement of observed and curve values.

Lauraceae.—A rather complex system of flower behavior exists in the avocado, *Persea americana* Miller, in which flowers perform first as one sex and later as the other. Interplanting of different varieties was studied by Wolfe et al. (1949) to learn if pollination were important through nearness of reciprocating varieties in fruit setting. Data were given for the determination of fruit-set on three varieties. An increase of fruit-set for the Linda variety was found with increase in distance, however, instead of a decrease. Curves were drawn to show the set of fruit for the Taylor and Wagner varieties (Fig. 84). Slight decreases in fruit-set with increases in distance from reciprocating varieties were found for the Taylor and the Wagner varieties. Row distances (may be counted as of 25 feet) greater than five appear to have had little effect on pollination as measured by fruit-set. Close alignment of observed and curve values is lacking. Insects are presumed to be the agents of pollination.

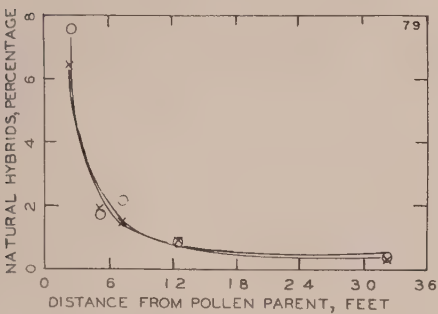

Fig. 79

Incidence of hybridization of lima beans. Upper curve represents data from 1950. Lower curve represents data from 1952 (data from Allard).

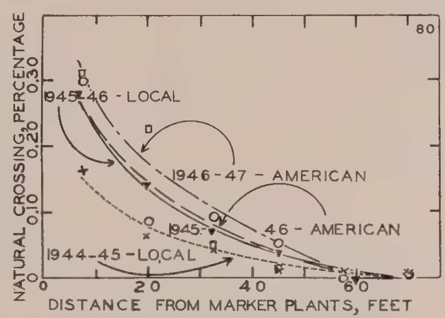

Fig. 80

Incidence of natural crossing in cotton (data from Afzal and Khan).

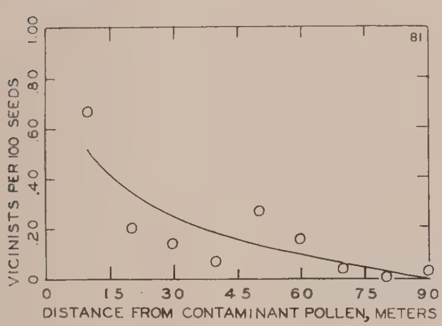

Fig. 81

Incidence of natural crossing in cotton. Barred line represents data from each distance block.
Solid line represents data from within block (data from Green and Jones).

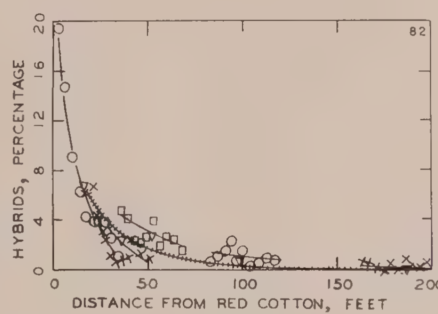

Fig. 82

Incidence of natural crossing cotton (data from balls).

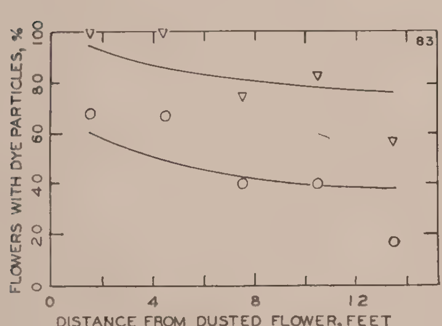

Fig. 83

Distribution of methylene blue among cotton flowers by bumble bees.
Upper curve represents data from upland cotton.
Lower curve represents data from Asiatic cotton (data from Stephens and Finker).

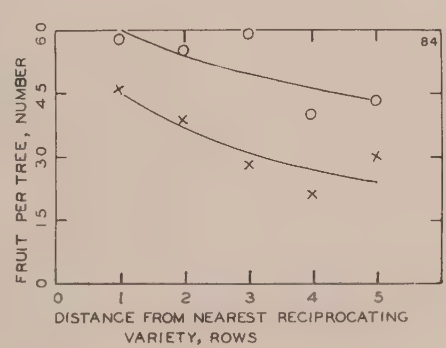

Fig. 84

Incidence of avocado fruit-set at distances from nearest reciprocating variety.
Upper curve represents data from the Taylor variety.
Lower curve represents data from the Wagoner variety (data from Wolfe, et al.).

In studying the effectiveness of honeybees for pollination of the avocado more honeybees and more fruit per tree were reported by Wolfenbarger (1955) near a 64-colony apiary than 1000 feet away. From the regression formula given a curve was drawn (Fig. 85). Calculated yields of fruit, bushels per tree, were 2.38 within 125 feet, 1.26 in the 500–625 foot zone and 0.94 in the 100–1125 foot zone from the apiary. The regresssion curve was significant as something other than zero, thus indicating a satisfactory agreement of observed and curve values.

Oleaceae.—Pollen grains falling from white and green ash trees, *Fraxinus americana* L., and *F. pennsylvania* var. *lanceolata* (Borkh.) Sarg. were counted by Wright (1952). Since no pronounced differences were found between different days or different species averages of these were obtained for each of the distance classes and used for drawing a regression curve (Fig. 86). A rapid rate of regression extended to near 200 feet from the pollen source. Lower counts were made at distances of 200 to 400 feet. There is close agreement of observed and curve values. Wind was the agent of dispersion.

Polemoniaceae.—Two color variations of *Linanthus parryae* (Gray) Greene were observed by Epling and Dobzhansky (1942). This plant is presumed to be insect-pollinated but its pollination mechanism is actually unknown. Color composition in a population of the plants was altered by contamination from nearby pollen sources of the opposing color. The incidence of contamination is shown in Fig. 87. Most contamination was found within several hundred feet. Some contamination, however, was found to two miles. A straight-line regression curve by untransformed values was acceptable for use with these data. There is fair agreement of observed and curve values.

Cucurbitaceae.—Effects of honeybees in distributing pollen among watermelon, *Citrullus vulgaris* Schrad., bloom were measured by Parris and Haynie (1950, unpublished 1951). Melon yields were found to decrease as the distance from the colonies increased. Two regression curves were drawn, one for each of the two years (Fig. 88). Melon yields were greater in 1950 than in 1951, as is shown by the positions of the curves. Similar rates of curvilinearity, however, are evident by the two curves. This indicates similar effects of honeybees in pollen distribution at nearby distances during each of the two years. At about 600 feet from the field margins the curves reach a more flattened slope indicating that watermelon production at that distance was affected little or none by the honeybees. There is fair agreement of observed and curve values.

Compositae.—Honeybees were found by Furgala (1954) to have increased the yields of sunflower, *Helianthus* sp., seed. Plants nearest the apiary yielded more than plants 1000 feet distant. From the figure given, data were taken to show the yields of seed per acre for computation of a regression formula, the curve of which is shown in Fig. 89. Curvature of the regression line is greater to distances of about 400 feet after which the slope is flattened. This indicates that honeybees influenced seed but little at distances in excess of about 400 feet.

Guayule, *Parthenium argentatum* Gray, pollen is affected by gravity

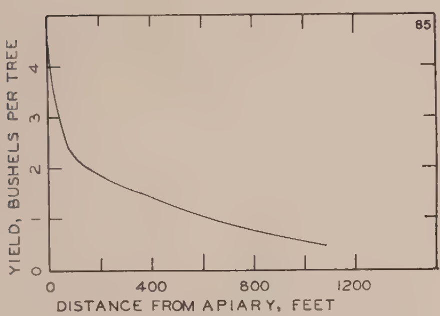

Fig. 85

Incidence of avocado fruit yield about an apiary (data from Wolfenbarger).

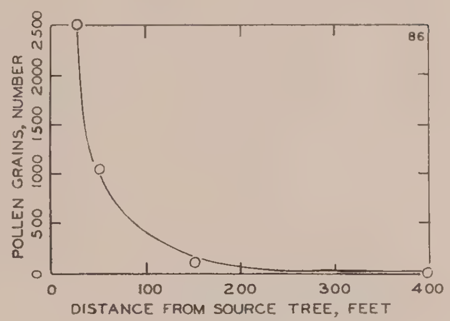

Fig. 86

Dispersion of ash pollen (data from Wright).

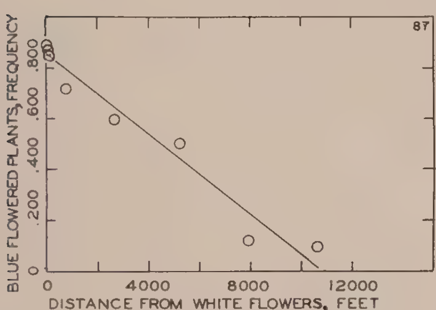

Fig. 87

Incidence of hybridization of blue-flowered *Linanthus* plants (data from Epling and Dobzhansky).

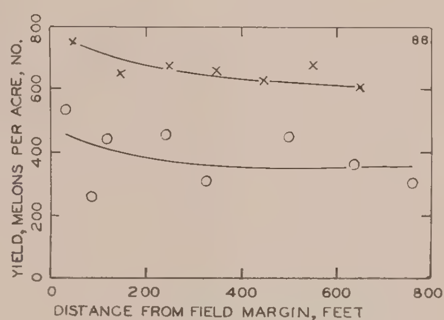

Fig. 88

Incidence of watermelon yield at distances from an apiary.

Upper curve represents data taken in 1950. Lower curve represents data taken in 1949 (data from Parris and Haynie).

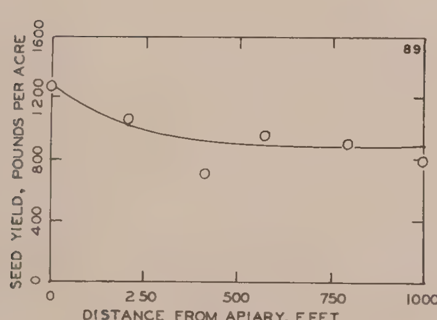

Fig. 89

Sunflower seed yield at distances from an apiary (data from Furgala).

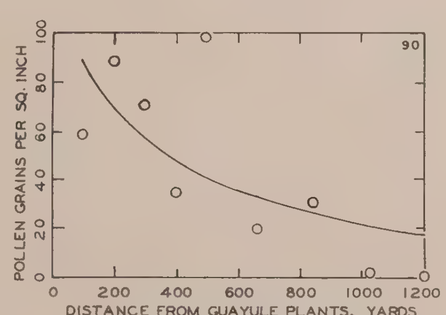

Fig. 90

Dispersion of guayule pollen (data from Gardner).

more than many other pollens. Guayule pollen, however, was reported by Gardner (1946) to disperse several hundreds of yards (Fig. 90). Guayule pollen was believed by Gardner (1946) to fall to the ground as soon as wind pressure is released. A low level of pollen deposition was observed to fall at distances in excess of 1000 yards. Wide variations in the data prevent close agreement of observed and curve values.

Cichoriaceae.—In his studies on the dispersion of organisms Brownlee (1911) found that seeds of *Apargia hispida* L. (Willd.) were dispersed in terms of feet. One set of observations was made on a "lower terrace"; the other on an "upper terrace". A regression curve was drawn from the data given for each set of observations (Fig. 91). Although more seeds were observed on the "lower terrace" than on the "upper terrace" the rates of dispersion were similar. Zero seeds were reached at near 26 feet on the "lower" and near 20 feet on the "upper terrace".

Kingdom Animalia

Littorinidae.—A mollusc, *Littorina rudis* de Geer, was found by Brownlee (1911) to disperse in terms of inches from the release point. Observations recorded on the numbers of released specimens at distances from the release point were used for the derivation of a formula for calculation of the regression rate. Reference is so often given to this early publication that it may be termed a classic in the field. From the data given, a semi-logarithmic formula was computed and the curve is shown in Fig. 92. All observations were made within six inches of the release point. Zero organism was reached at near five and one-fourth inches, according to the regression curve. Dispersion was accomplished by crawling.

Daphniidae.—Water-fleas, *Daphnia culex* de Geer, distributed themselves within inches of their source, according to Brownlee (1911). Two sets of observations, A and B, were made on the dispersion of this crustacean (Fig. 93). Similar rates of dispersion were found for both sets of observations. The numbers of water-fleas were slightly higher in the B set than in the A set which gave it a slightly higher position on the graph. A maximum distance of about nine inches is shown for dispersion of the water-flea. Dispersion was by crawling.

Locustidae.—Studies on the dispersion of grasshoppers over bare soil were reported by Munro and Telford (1942). Nymphs, about 75 per cent of which were the two-striped grasshopper, *Melanoplus bivitattus* Say, and 25 per cent were divided between the migratory *M. mexicanus* Sauss., and Packards grasshopper, *M. packardi* Scudder, were released. Recaptures were made two and one-fourth hours later, after the insects had had the opportunity to move in any direction. All recaptures were within 400 feet of the release point (Fig. 94). The regression curve shows that three grasshoppers might have been expected at 400 feet from the release point although none was found at that distance. Close agreement of observed and curve values was lacking. Most recoveries were made northwest of the release point, fewest southeast, and intermediate numbers were taken northeast and southeast of the release point.

Grasshoppers tagged with radiophosphorus tended to remain near

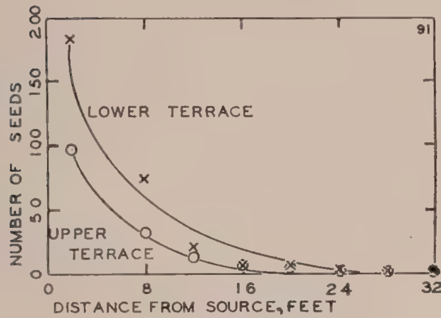

Fig. 91
Dispersion of *Apargia* seeds (data from Brownlee).

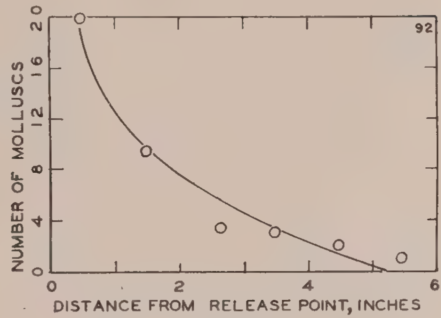

Fig. 92
Dispersion of *Littorina* from the release point (data from Brownlee).

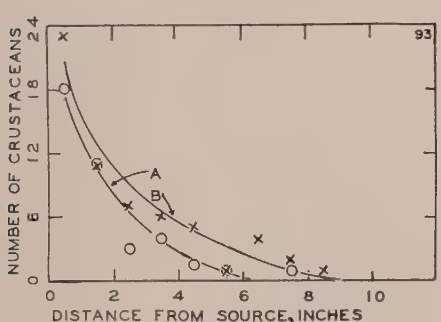

Fig. 93
Dispersion of water-fleas
Curves A and B represent two sets of observations (data from Brownlee).

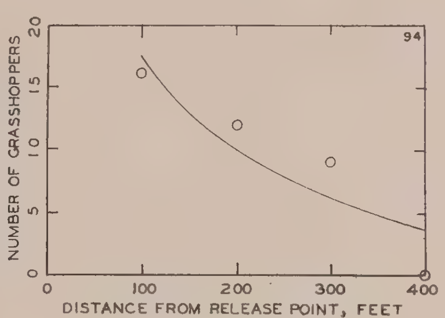

Fig. 94
Dispersion of grasshoppers over bare ground (data from Munro and Telford).

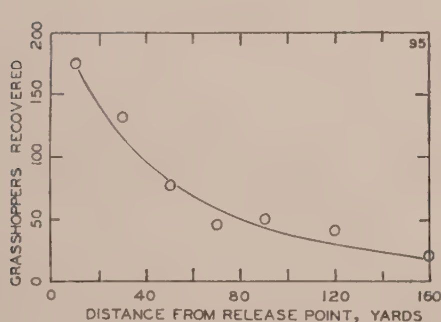

Fig. 95
Dispersion of grasshoppers from release site (data from Riegert).

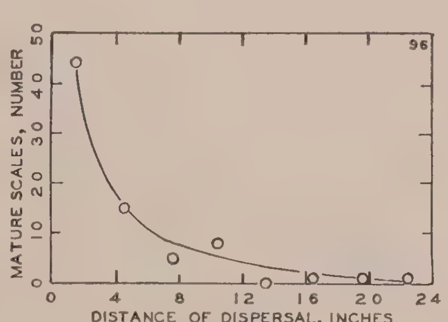

Fig. 96
Dispersion of scurfy scale crawlers (data from Hill).

the release point, according to Riegert et al. (1954). Nymphs of the fifth instar and adults of the *Melanoplus mexicanus mexicanus* (Sauss.) were treated with p^{32} and released in a area devoid of vegetation. After seven days recaptures of tagged and released grasshoppers were made to determine the distances of movement. A regression curve was drawn to show the dispersion distance (Fig. 95). Marked reductions were found in the number of grasshoppers recovered within 160 yards of the release site. Although 160 yards was the maximum distance under observation the regression curve indicates zero recovery was at some distance in excess of 160 yards. There is fair agreement of observed and curve values. Adults were reported to have moved with the wind; the nymphs against the wind. Dispersion is presumed to have been accomplished by crawling although there may have been some flights by the adults.

Coccidae.—Most scurfy scale, *Chionaspis furfura* Fitch, crawlers remained within three inches of their origin, according to Hill (1952). Twenty-four inches was the greatest distance of travel observed. A regression curve was drawn to show the rate of dispersion (Fig. 96). A fairly rapid rate of dispersion was observed in the distance crawled to near 12 inches followed by a reduced rate at distances in excess of 12 inches. There is fair agreement of observed and curve values. The mode of dispersion was by crawling.

Aphididae.—Distribution of the green peach aphid, *Myzus persicae* (Sulz.), was more abundant in an earlier planting of potatoes than in a later planting, according to Klostermeyer (1953). A heavy population of winged aphids developed on the potatoes planted early part of which dispersed to the potatoes planted later. A regression curve was drawn (Fig. 97) to show the aphid population gradient based on data obtained on the count days of July 16 and August 1. A rapid rate of reduction in numbers of aphids was found from the outside to 40 rows from the early potatoes after which the reduction became less. Dispersion extended, however, to some distance more remote than 160 rows, the maximum distance observed. There is fair agreement of observed and curve values. Dispersion was by flight, aided perhaps, by air currents.

Cicadellidae.—In studies of the beet leafhopper, *Circulifer tenellus* (Baker), Lawson et al. (1951) found that gravid females may travel many miles. A regression curve was drawn to show the progressive increase in the percentage of females carrying eggs (Fig. 98). There were 20 per cent more gravid females that had traveled 50 miles than of those that had not traveled. A straight-line connects the three observed values very closely. Non-gravid females tended to fly to other areas. From discussions by the authors and the data given it is evident that females became gravid after the flight began. The mode of dispersion is by flight.

Although the six-spotted leafhopper, *Macrosteles divisus* Uhl., feeds on many plants it exhibits preferences for certain plants. The carrot is a preferred host plant. Winter wheat plants were found more heavily infested adjoining a carrot field in a report by Hervey and Schroeder (1947). Data were obtained by sweeping plants at distances from the carrot field and were used for computation of a regression

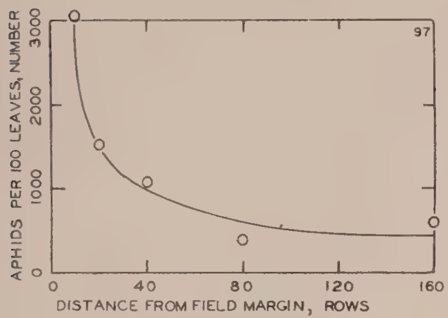

Fig. 97

Incidence of *Myzus persicae* in late potatoes (data from Klostermeyer).

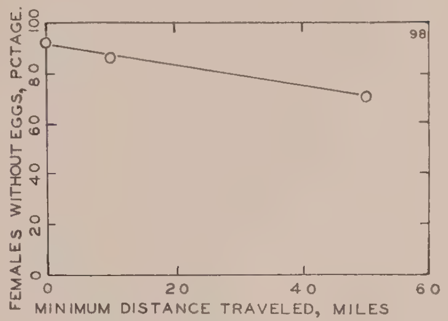

Fig. 98

Dispersion of female beet leaf hoppers carrying eggs (data from Lawson, et al.).

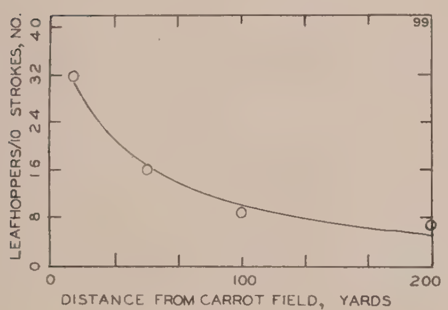

Fig. 99

Incidence of the six-spotted leafhopper adjoining a carrot field (data from Hervey).

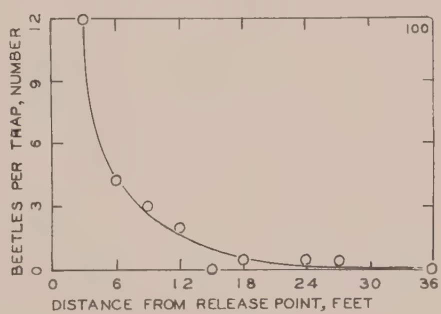

Fig. 100

Dispersion of *Agriotes obscurus* from the release site (data from Roebuck, et al.).

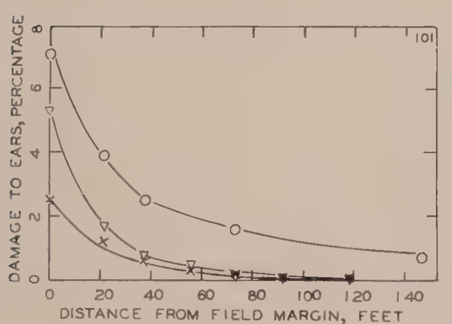

Fig. 101

Incidence of injury to corn by the Japanese beetle.

Upper curve represents data from 1951.
Middle curve represents data from 1953.
Lowest curve represents data from 1952 (data from Woodside).

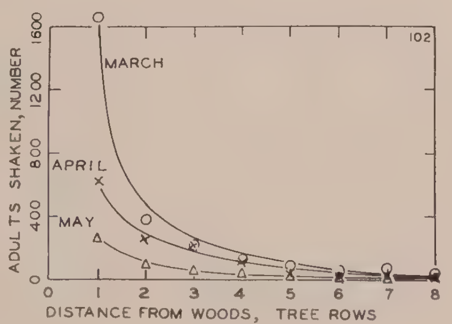

Fig. 102

Abundance of plum curculio at distances from woodlands (data from Quaintance and Jenne).

curve (Fig. 99). About one-sixth as many six-spotted leafhoppers were taken at 200 as at 10 yards from the carrot field. There is a fair agreement of observed and curve values. As evidenced by the curve a zero count would be expected at some distance in excess of 200 yards. Dispersion was by flight.

Elateridae.—Click beetles, *Agriotes obscurus* L., were released by Roebuck et al. (1947) at a point in a meadow with opportunities to disperse in all directions. One hundred of a total of 448 beetles released were recaptured at distances from the release point. A regression curve was drawn from the data given (Fig. 100). A low incidence of recovery was reached, according to the curve, at 24 feet. This curve and conclusions reached by the authors indicate that adults of the species remain near the site of their origin. Each field was considered, ". . . a self-contained habitat." and depended on its own beetles for, ". . . gradually building up a high population." There is fair agreement of observed and curve values. Dispersion was by walking or running.

Scarabaeidae.—Japanese beetle, *Popillia japonica* Newman, damage to corn was reported by Woodside (1954) to decrease as the distance from the field margin increased. Woodland or fence-row plants may be hosts for concentrations of beetles. Such concentrations of beetles disperse to inflict severe damage if corn is silking when the beetles are abundant. A curve was drawn for each of the three years for which data were given, allowing 3½ feet for calculating row distances (Fig. 101). Distances of 100 feet from field margins show great reductions in damaged corn as compared with zero distance. There is close agreement of observed and curve values. Dispersion of the beetles was by flight.

Curculionidae.—Peach trees in the outer rows of peach orchards adjoining woodlands are more heavily infested with the plum curculio, *Conotrachelus nenuphar* (Herbst.), than are the trees more distant from woodlands. Relative abundances of beetles were reported by Quaintance and Jenne (1912) at distances from their overwinter quarters, the woodlands. Curves were drawn to show results from March, April and May collections (Fig. 102). More beetles were shaken in March than in April, and more in April than in May. The lowest number of beetles was shaken from trees in the eighth row each month. There is fair agreement of observed and curve values. Dispersion was by flight.

In a study on the biology of the sweet potato weevil, *Cylas formicarius elegantulus* (Sum.), Cockerham et al. (1945) gave some data on dispersion of the adults. Many weevils were caught in flight which could explain new infestations. This was considered of more importance than transportation of infested plants or sweet potatoes Uninfested sweet potato plants were set at distances from the sources of infestations and cultivated through the crop season. Results were based on percentages of plants infested at distances from the source. A curve was drawn to show the trend (Fig. 103). These data show that a sweet potato planting within a mile of a source of the weevil is likely to become infested. Within the maximum distance (1760 yards) under observation the disagreement of observed and curve values do not show a definite relationship between infestation and distance from a known source of weevils. Dispersion was by flight.

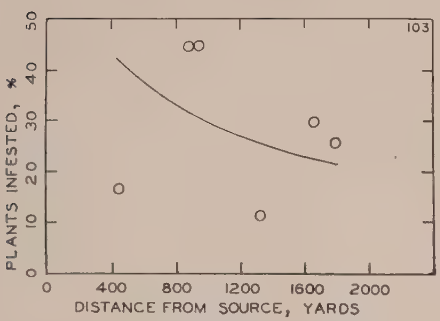

Fig. 103

Incidence of sweet potato plants infested by the sweet potato weevil at distances from the source (data from Cockerham, et al.).

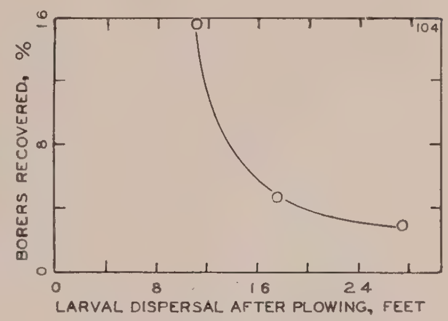

Fig. 104

Dispersion of European corn borer larvae after plowing (data from Huber, et al.).

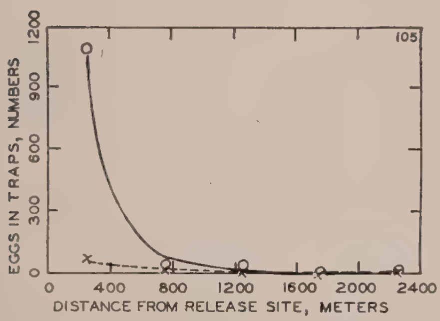

Fig. 105

Number of eggs per trap at distances from release site of *Aedes aegypti.*

Upper curve represents data from August release.

Lower curve represents data from September release (data from Wolfinsohn and Galun).

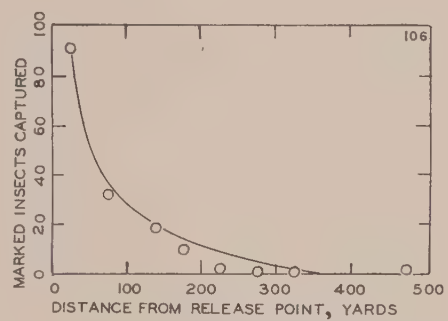

Fig. 106

Recapture of *Aedes albopictus* at distances from the release site (data from Bonnet and Worcester).

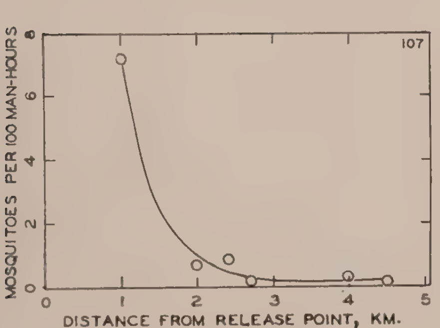

Fig. 107

Dispersion of forest mosquitoes from release site (data from Causey and Kumm).

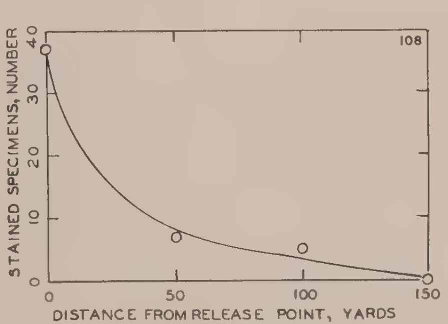

Fig. 108

Dispersion of stained *Aedes polynesiensis* (data from Jachowski).

Pyralidae.—European corn borer, *Pyrausta nubilalis* (Hbn.), larvae were found by Huber et al. (1928) to move in terms of feet after a plowing operation. An observation of 38.5 per cent of borer larvae recovered "adjacent" to the source was omitted in computing the regression curve (Fig. 104). Three and one-half percent of the borer larvae moved 27.5 feet. Very close agreement of observed and curve values was found. Dispersion was by larval movement, and consisted of crawling or burrowing.

Culicidae.—In studying dispersion of *Aedes aegypti* (Linn.) Wolfinsohn and Galun (1953) released 45,000 gravid females in August and 28,000 gravid females in September. Releases were made in a desert area in Southern Israel free of wild *A. aegypti* and apparently free of attractive areas for egg deposition by the released mosquitoes. Jars of four liter capacity nearly filled with water were placed over a 2.5 km. radius about the release site for egg deposition by the mosquitoes. Examinations were made for any eggs in each jar 1, 2, and 3 days after the release of the gravid females. Mean numbers of eggs per jar were obtained for each experiment for each of five distance radii and from these regression curves were drawn (Fig. 105). Eleven hundred eggs per trap were found within 500 m. following the August release. This compares with 71.1 found following the September release. As a result of those wide differences the initial portions of the regression curves are very dissimilar. Beyond about 1200 m., however, the curve segments are similar and show low numbers of eggs per trap.

Release-recapture experiments were conducted by Bonnet and Worcester (1946) to determine the dispersion of *Aedes albopictus* (Skuse). A regression curve drawn from the data given shows the dispersion range was in hundreds of yards (Fig. 106). A low incidence of recapture was reached within 225 yards of the release point. There is fair agreement of observed and calculated values. Dispersion was by flight aided, perhaps, by air movements.

Staining, release, and capture of stained specimens were methods used by Causey and Kumm (1948) in Brazil to study the dispersion of forest mosquitoes. *Aedes serratus* (Theob.), *A. scapularis* Roudani, *A. crinifer* (Theobald), *Psorophora ferox* (Humb.) and "other species" were used for the experiments. Data on all species and from all directions were pooled for making the calculations for the regression curve (Fig. 107). There was a rapid rate of decrease in the number of stained specimens to about two miles from the release point although stained specimens were taken to distances of 4.7 km. Dispersion was by flight, aided possibly by air movements.

A bush mosquito, *Aedes polynesiensis* Marks, is a vector of nonperiodic filariasis, a potential vector of dengue and is an important pest mosquito in American Samoa, according to Jachowski (1954). Field collections of *A. polynesiensis* were taken, marked with dye, released, and a portion of those released were recaptured to determine the dispersion distance. From data given by Jachowski (1954) (150 yards was the figure used for the "100" yards given) a regression curve was drawn (Fig. 108). Most specimens retaken were within 100 yards of the release site. A zero was given for the "100 yard" distance but the curve value was 0.4 mosquito. The dispersal distance of *Aedes poly-*

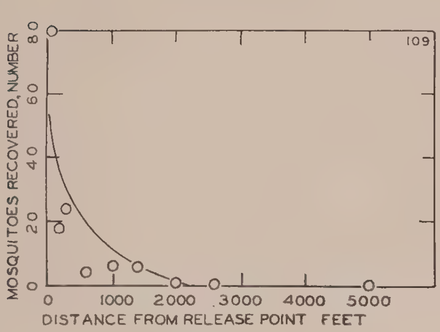

Fig. 109

Dispersion of marked mosquitoes in the sub-Arctic (data from Jenkins and Hassett).

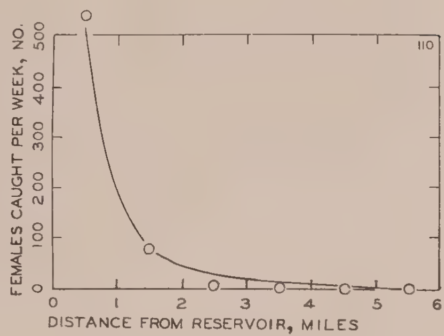

Fig. 110

Incidence of *Anopheles quadrimaculatus* about a breeding site (data from Eyles).

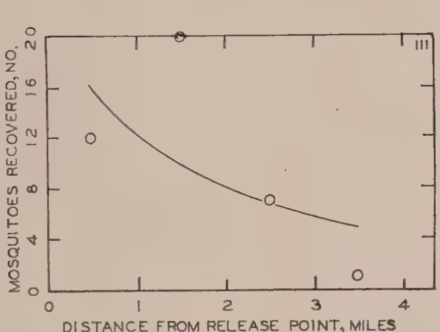

Fig. 111

Dispersion of *Anopheles pseudopunctipennis* from the release site (data from Rickard).

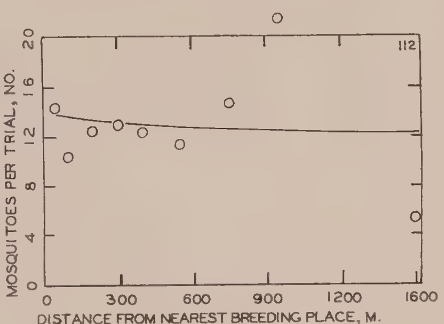

Fig. 112

Incidence of anopheline abundance about the nearest breeding site (data from de Zulueta).

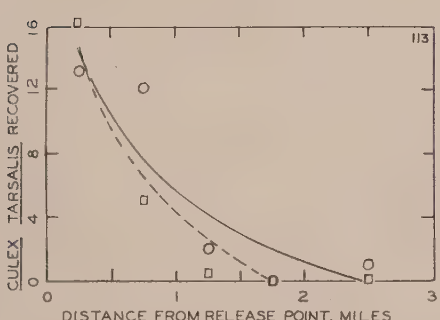

Fig. 113

Dispersion of *Culex tarsalis* from the release site.

Solid line represents number of mosquitoes collected.

Broken line represents number of *C. tarsalis* on per square mile basis (data from Reeves, et al.).

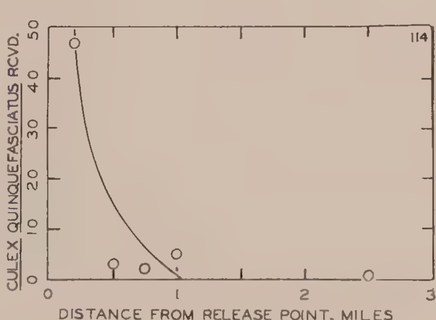

Fig. 114

Dispersion of *Culex quinquefasciatus* at distances from the release site (data from Reeves, et al.).

neisiensis is very limited compared with certain other mosquitoes, even of the same genus. *A. sollicitans* (Wlk.) specimens, for example, were found by MacCreary and Stearns (1937) to disperse in terms of miles over water in Delaware Bay. Dispersion was by means of flight, aided possibly by air movement.

Sub-Arctic mosquitoes, *Aedes communis* (Deg.), were marked with radiophosphorus and released for dispersal as reported by Jenkins and Hassett (1951). Of 3,000,000 released a very small recovery, 141 (0.004, 7 per cent) was made. These recoveries were taken at distances from the release point as indicated in Fig. 109. The regression curve reached zero at near 2,000 feet. There is poor agreement of observed and curve values. Most sub-arctic mosquitoes remain near the release point according to these observations. The term, "effective dispersal" was used for distance to ¼ mile owing to paucity of recoveries in excess of 1400 feet from the release point. Further reference is made to the scarcity of collected specimens at greater distances under Generalization. Dispersion was by flight, aided possibly by air movement.

In an area where the malaria mosquito, *Anopheles quadrimaculatus* Say, was breeding in great abundance an opportunity was afforded Eyles (1945) to make studies on long-range dispersal of the species. From the counts of mosquitoes in "stable type" stations for the first ten weeks at different distances from the reservoir a regression curve was drawn (Fig. 110). A rapid rate of reduction in the numbers of mosquitoes fell to low levels at distances greater than two miles from the breeding area. There is fair agreement of observed and curve values. Dispersion was by flight, aided possibly by air currents.

Anopheles pseudopunctipennis Theobald specimens were released for dispersal and recapture by Rickard (1928, after Eyles 1944). Over 10,000 females were stained with aniline dyes and released at three sites. Only 40 stained specimens were recovered. A regression curve was drawn from the recoveries, however, to show the rate of dispersion (Fig. 111). It is evident from the regression curve that some specimens dispersed to some distance in excess of four miles. Owing to insufficient data, however, others are needed to substantiate the regression curve. Dispersion was by flight, aided possibly by air currents.

Long distance dispersion, as from the breeding area, and short distance dispersion, as toward a source of blood, were recognized by de Zuleta (1950) as distinct habits of neotropical anopheline mosquitoes, *Anopheles perryaussi* Dyar & Knab, *A. pessoai* Galvao & Lane, and *A. parvues* (Chagas.). Data were given, however, on long distance dispersal from the nearest breeding area, from which a regression curve was drawn (Fig. 112). Only a slight reduction is indicated by the curve over the 1600 meter distance. There is much scatter of observed values. Dispersion is by flight, aided possibly by air movement.

In recognition of the need for more definite information in order to arrive, at ". . . a more tentative practical limit for control measures . . ." Reeves et al. (1948) released and made recoveries of *Culex tarsalis* Coq. From the data given two regression curves were drawn (Fig. 113). One curve represents both sexes of *C. tarsalis* caught within given radii of the release point. The other curve represents recovered insects

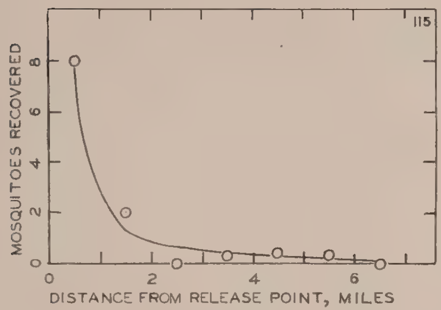

Fig. 115
Dispersion of rice field mosquitoes (data from Quarterman, et al.).

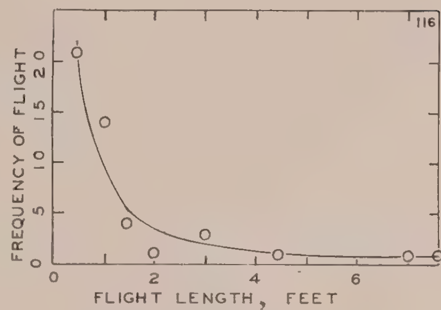

Fig. 116
Flight lengths of hover flies foraging among turnip blossoms (data from Bateman).

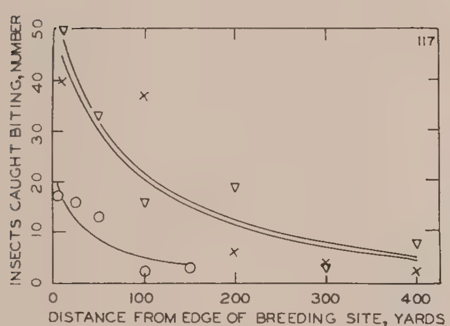

Fig. 117
Incidence of biting *Culicoides grahamii* at distances from breeding sites. Different curves represent data from different areas or different times (data from Nicholas).

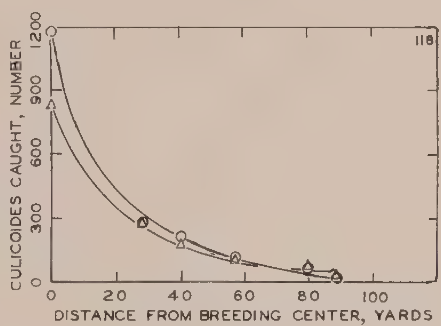

Fig. 118
Culicoides caught at distances from a breeding area.
Upper curve represents data for males.
Lower curve represents data for females (data from Kettle).

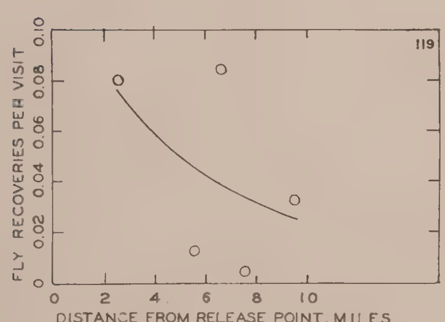

Fig. 119
Dispersion of blackflies (data from Dalmat and Gibson).

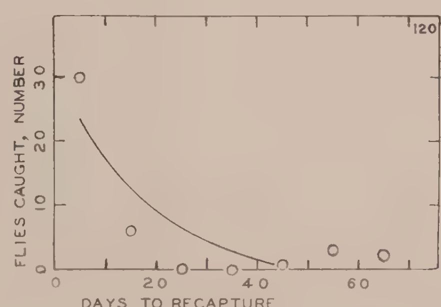

Fig. 120
Time between release and recovery of blackflies (data from Dalmat and Gibson).

on a per square mile basis. A more rapid rate of reduction is shown where the rate of recovery is based on a "per square mile" basis than on insects caught within given radii. Close agreement of observed and curve values is lacking. The regression curves show a trend, however, in which about ⅓ as many *Culex tarsalis* may be expected at two as at one-fourth mile from the release site. Dispersion was by flight, aided possibly by air movements.

Fluorescent dyes were used by Reeves et al. (1948) in studying mosquito dispersion. Recovery of *Culex quinquefasciatus* Say was made to two and one-half miles from the release point. Recovered were 28 females and 30 males which were pooled for determining the regression curve (Fig. 114). Most mosquitoes were recovered within one mile of the release point. There is poor agreement of observed and curve values, but a trend is indicated for the species. Dispersion was by flight, aided possibly by air movement.

Radioactive phosphorus was used by Quarterman et al. (1955) for marking rice-field mosquitoes, *Psorophora confinnis* Lynch-Arribalaza and *P. discolor* Coq. Owing to the comparatively low recoveries made 39 *P. confinnis* and 5 *P. discolor* the data from both species were pooled for determining a regression curve. Number of mosquitoes per trap was the basis used for drawing the regression curve (Fig. 115). A rapid rate of regression was found to near two miles after which the curve continued to low levels to near six miles. Dispersion was by flight, aided possibly by air movement.

Syrphidae.—Hover flies visiting turnip blossoms were found by Bateman (1947a) to move short distances in flying from one flower to another. A regression curve was drawn to show the frequencies of flight lengths (Fig. 116). Flight lengths of less than one foot were most frequently observed. Flights in excess of two feet were infrequent, although some flights were in excess of seven feet. There is fair agreement of observed and curve values. Dispersion was by flight. There was some doubt, according to Bateman (1947a), as to whether the slow or "foraging" flights and soaring flights of the hover flies serve the same purpose as homing flights with the social insects of the Apidae. Hover flies are considered relatively unimportant as pollinating agents for most crop plants.

Chironomidae.—Biting of the chironomids, *Culicoides grahami* Aust., and *C. austeni* Carter, Ingram and Macfie became less frequent with increasing distance from a breeding site, according to Nicholas (1953). At intervals along a line at right angles to the boundary of a breeding site "fly-boys" were placed to catch the flies which came to bite them. Estimates were thus obtained of the biting density at distances from the breeding site. Three regression curves were drawn from the given data (Fig. 117). Two regression curves, one from data taken December 2 and one from data taken December 3, are very similar. A curve drawn from data taken November 3 has slightly greater curvature than those drawn from the December data. Biting at a distance of 400 yards was much less than biting nearer than 100 yards. Closer alignment of observed and curve values is desirable where it may be obtained. A curve drawn from data obtained on December 1 actually showed an increase in the biting rate with increased distance from a breeding site. Dispersion of the insect was by flight.

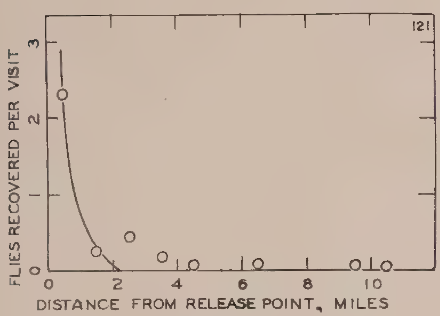

Fig. 121

Dispersion of *Simulium* flies at distances from the release site (data from Dalmat).

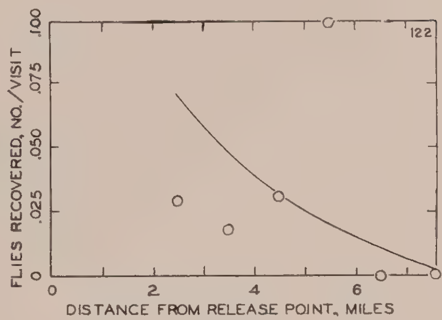

Fig. 122

Dispersion of Simulium flies at distances from the release site (data from Dalmat).

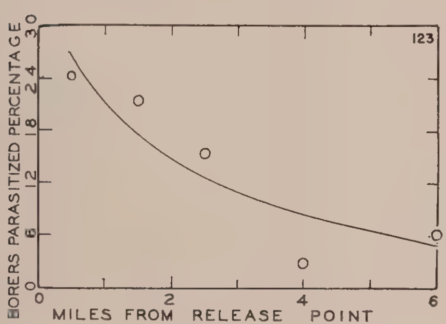

Fig. 123

Incidence of parasitization of the European corn borer by *Lydella stabulans grisescens* (data from Baker, et al.).

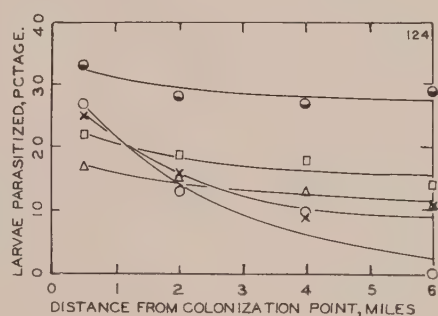

Fig. 124

Incidence of parasitization of European corn borer by *Lydella stabulans grisescens*. Open circles, X characters, triangles, squares and half black circles represent data from 1943, 1944, 1945, 1946 and 1947, respectively (data from MacCreary and Rice).

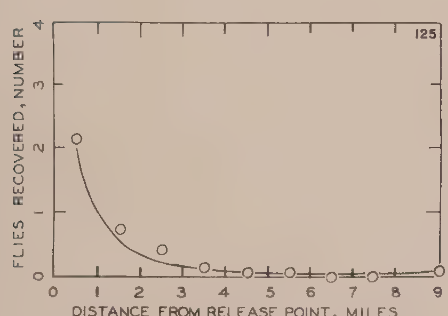

Fig. 125

Dispersion of *Callitroga macellaria* from release on rural site (data from Quarterman, et al.).

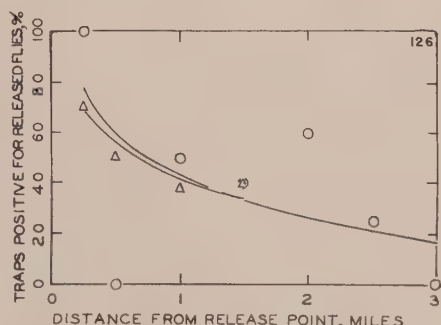

Fig. 126

Dispersion of yellow-eyed mutant strain *Callitroga macellaria* from release site on "city garbage dump" (longer curve) and in "an urban area" (shorter curve) (data from Quarterman).

A considerable amount of data was reported by Kettle (1951a, 1951b) on the spatial distribution of *Culicoides impunctatus* Goet. around its breeding areas. He found that the average distance dispersed by females was 81.4 and by males was 79.0 yards. Regression curves were drawn to show the regression rates for each sex (Fig. 118). Rapid decreases to low density levels were found within 100 yards of the breeding sources. Although the population density levels of male populations were higher nearer the breeding areas than the density levels of females the regression curves show that the populations tend to become equalized. Differences in the regression coefficients of the sexes were attributed by Kettle (1951a) to experimental error; hence, are more apparent than real. Further references are made to these exhaustive studies elsewhere.

Studies of flight and longevity of blackflies were made by Dalmat and Gibson (1952). In addition to the bites inflicted the species studied, *Simulium ochraceum* Walker, *S. metallicum* Bellardi, and *S. callidium* Dyar and Shannon, are carriers of *Onchocera volvolus* (Leuckart, Railbit & Henry) the causal factor of human onchocerciasis. Owing to the paucity of data on any one species the data were pooled from all species to determine a regression curve (Fig. 119). A rather rapid rate of regression is shown by the curve from 2 to 10 miles from the release point. There is much scatter of observed values indicated.

Data were given by Dalmat and Gibson (1952) on the time elapsed between release and recovery of blackflies. A regression curve was drawn to illustrate the rate of fly recovery to days after release (Fig. 120). A low rate of recovery was reached at 45 days after the release of stained flies. Some flies, however, lived longer than two months.

Data by Dalmat and Gibson (1952) on three species of blackflies from observations at two locations were pooled for computing a regression curve on simuliid dispersion (Fig. 121). Most flies were recovered within four miles of the release site. Very few flies were recovered between four and 11 miles. Closer alignment of observed and curve values would increase confidence in the trend line.

Dispersion studies on Simulium flies by Dalmat (1950) included distance ranges to a maximum of seven miles. The data on three species, *S. ochraceum* Walk., *S. metallicum bellardi* and *S. callidium* Dyar and Shannon of released flies were pooled as flies recovered "per visit" for calculating a regression curve (Fig. 122). The regression line reaches almost to zero at seven miles from the release point. Owing to the apparent high recovery observed at the 5½ mile distance point there is lack of close agreement of observed and curve values. Dispersion of the Chirononidae was by flight.

Tachinidae.—Species of this family are usually parasites of other insects. It is but an expected occurrence that the incidence of parasitization would be greater nearer the source of the parasite. This is especially true if the parasite is an introduced species. Some rather extensive studies on biological control of the European corn borer, *Pyrausta nubilalis* (Hbn.), were reported by Baker et al. (1949). They showed how the tachinid parasite *Lydella stabulans grisescens* R. D. was most abundant nearest a release point. Data were taken 11 years after the introduction of the parasite to show the rate of dispersion

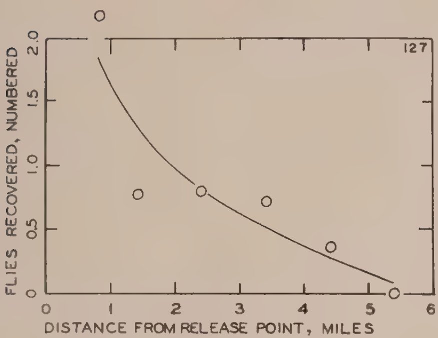

Fig. 127
Dispersion of *Phormia regina* from the release site (data from Schoof and Mail).

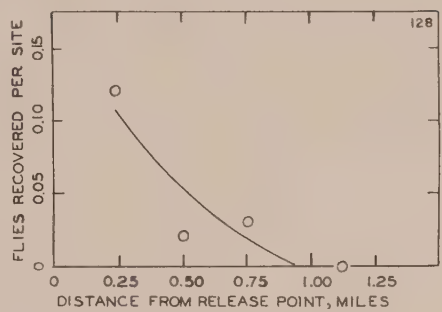

Fig. 128
Dispersion of *Phormia regina* from the release site (data from Schoof and Siverly).

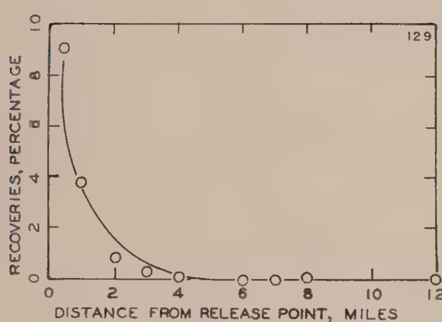

Fig. 129
Dispersion of *Phormia regina* from the release site (data from Lindquist, et al.).

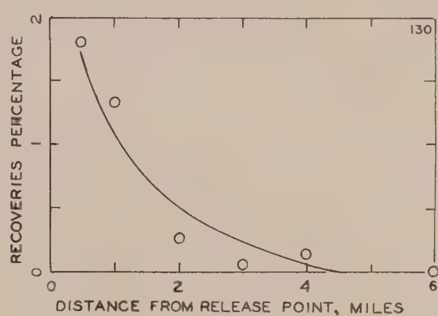

Fig. 130
Dispersion of *Phaenicia sericata* from the release site (data from Lindquist, et al.).

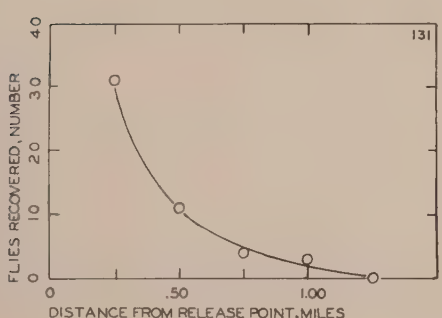

Fig. 131
Dispersion of *Phaenicia* sp. from the release site (data from Schoof and Siverly).

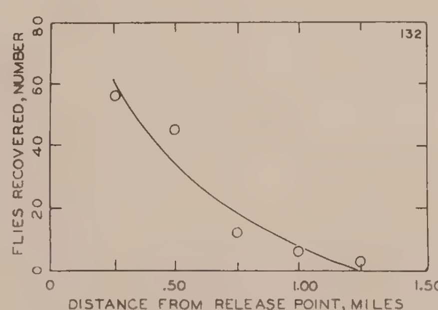

Fig. 132
Dispersion of the housefly from an urban area release site (data from Schoof and Siverly).

(Fig. 123). The curve shows that zero percentage parasitization was reached at some distance greater than six miles. There is either a low observed figure at four miles or a high one at six miles distance making wide differences between observed and curve values. Dispersion was by flight.

Measures of the effectiveness of *Lydella stabulans grisescens* in parasitization of the European corn borer, *Pyrausta nubilalis* (Hbn.), were determined by MacCreary and Rice (1949). Parasites were released in 1941 and became established. Parasitization records were obtained around the release point to a distance of six miles. Records obtained from each of five years were used in computations before drawing five regression curves (Fig. 124). The lowest percentage of parasitization is shown for each year at six miles from the release site according to the curves. Successively larger percentages of parasitization were found at the six mile distance in 1944 and 1945 following the first records in 1943. The 1943 regression curve has the most slope, followed by the 1944 curve. These are considered to show the most effect of the dispersing tachinid population. By 1945 six miles was too short to show much effect of distance. Similar curvilinearity of the results for 1945, 1946, and 1947 show fluctuations between years as measured at distances from the release site. Gentleness of curve slopes indicates that parasitization was influenced little after 1945 by the original release of parasites. Part of the results shown in Fig. 124 are effects of secondary, tertiary and later cycles of parasite introduction. Part of the parasitization, therefore, is attributed to intensification in numbers of organisms at an origin in a manner similar to that described by Fracker (1936). Dispersion is by flight except for passive transportation by other insects as agents.

Calliphoridae.—Radioactive chemicals in the food and dyes dusted on the flies were used by Quarterman et al. (1954a) to study fly dispersion. Releases of marked flies were made at five locations. A summarization of the blow fly *Callitroga macellaria* (F.) recoveries per trap at the different distances was used to draw a regression curve (Fig. 125). A low level of fly recoveries was reached within four miles of the release sites. Low recoveries continued to nine miles from the release point. There is fair agreement of observed and curve values.

A re-emphasis of sanitation or prevention of breeding sources was given by Quarterman et al. (1949). Investigations were made of the dispersal of a yellow-eyed mutant strain of *Callitroga macellaria* (F.) laboratory reared flies by releases of the insects on a city garbage dump where many blow flies were breeding, and also in a residential section of a city where flies were few. Traps were placed at distances from release sites for recovering flies. Two regression curves were drawn from the data given (Fig. 126). The two curves have very similar rates of slope although close agreement of observed and curve values is lacking. The curves suggest dispersion to some distance in excess of six miles which was the maximum distance of trap placements. The authors found (a) that flies dispersed from a favorable breeding area, and (b) the flies dispersed from the release site in all directions.

Radioactive milk was fed to *Phormia regina* (Meig.) by Schoof and

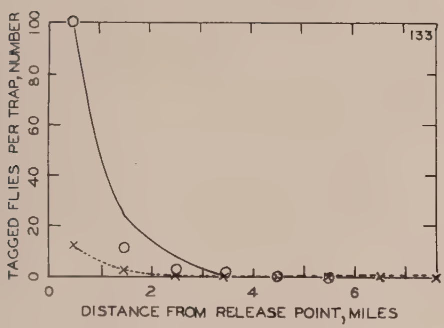

Fig. 133

Dispersion of the housefly
Solid line represents data from a release site, from April 30 to May 15 releases.
Broken line represents data from five release sites, from June 20 to July 2 releases (data from Quarterman, et al.).

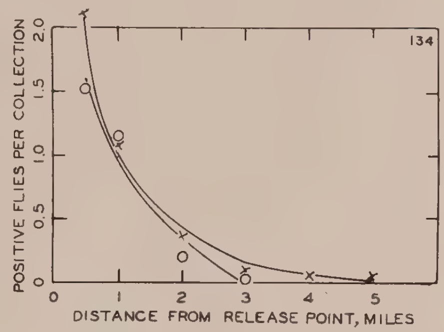

Fig. 134

Dispersion of the housefly from metropolitan release sites.
Upper curve represents data from September tests.
Lower curve represents data from June tests (data from Schoof, et al.).

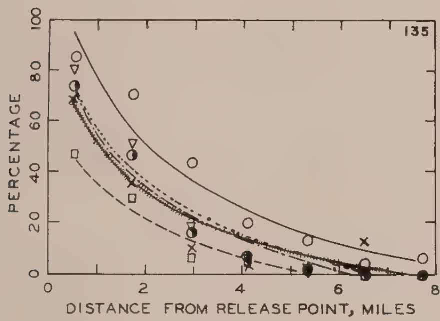

Fig. 135

Dispersion of the housefly from release sites.
Upper curve represents data from hog farm.
Lowest curve represents data from the rendering plant.
Barred curve represents data from meat packing concern.
Dotted curve represents data from the lettuce dump.
Curve with alternate dashes and dots represents data from the poultry farm (data from Schoof and Siverly).

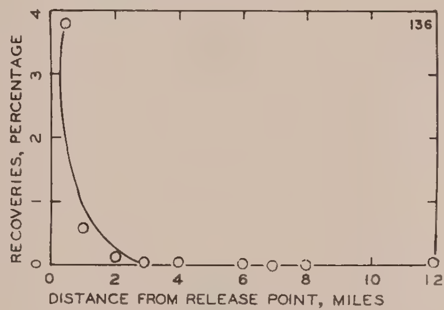

Fig. 136

Dispersion of the housefly (data from Lindquist, et al.).

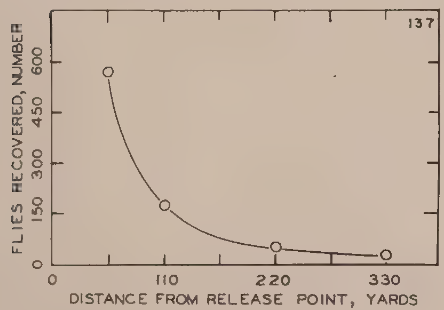

Fig. 137

Dispersal of flies from the release site (data from Wolfinsohn).

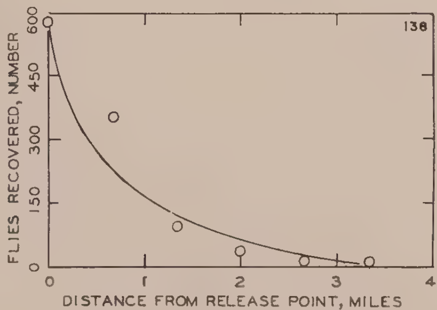

Fig. 138

Dispersion of the male tsetse flies (data from Jackson).

Mail (1953) for studying dispersion of the fly. Releases were made at two points. Data were pooled from all distance classes from both releases for drawing a regression curve (Fig. 127). Curve values were 1.81 and 0.08 flies at 0.8 and 5.4 miles, respectively, from the release point. One fly (not included in the regression computations) was recovered in the 10.0–10.9 mile zone from the Kanawha City release point. Close agreement of observed and curve values is lacking.

In studying the dispersion patterns of flies Schoof and Siverly (1954a) obtained some data on distances to which *Phormia regina* Meig. and *Callitroga macellaria* (F.) moved. These flies were tagged with p^{32} in a milk diet. Since only four *C. macellaria* were recovered, no curve was drawn to show the results. A curve was drawn, however, to show recovery of *P. regina* Meig. (Fig. 128). All flies were recovered within three miles of the release site. Since but seven specimens were recovered and used to determine the curve in Fig. 128 one may question what form the curve would take if there had been more recoveries.

The blow-fly, *Phormia regina* (Meig.), was fed radioactive phosphoric acid and released by Lindquist (1951). A regression curve was drawn from the data given (Fig. 129). A low percentage of recovery was reached at near four miles from the release point. Zero recovery according to the curve values, was reached at near five miles.

The blow-fly, *Phaenicia sericata* (Meig.) was fed radioactive phosphoric acid and released by Lindquist et al. (1951). A regression curve was drawn from the data given (Fig. 130). A low rate of *P. sericata* recovery, 0.14 per cent, according to the curve value, was reached at four miles from the release site, with zero recovery near 4.5 miles.

In studies on dispersion data were given by Schoof and Siverly (1954a) on *Phaenicia* sp. These flies had been tagged with p^{32} and released. Numbers of the released flies were recovered by trapping operations. A regression curve was drawn from the data given (Fig. 131). Zero recovery was reached at 1.25 miles from the release point. Observed and curve values agree closely. There were 31 flies recovered at 0.25 miles and 0 fly at 1.25 miles from the release point. Further reference will be made to this subject under Generalizations. Dispersion of the Calliphoridae is by flight.

Muscidae.—In studying housefly, *Musca domestica* L., dispersion under urban conditions Schoof and Siverly (1954b) tagged flies by feeding them milk containing p^{32}. A regression curve was drawn to show the rate of regression (Fig. 132). The regression has a comparatively gentle slope. Zero recovery, according to the curve, is reached at near 1.25 miles from the release site.

Houseflies were tagged with radiophosphorus then released by Quarterman et al. (1954b) to study fly dispersal in a rural area. Two curves were drawn to show the recoveries, based on average number of flies per trap (Fig. 133). The two curves differ considerably, one shows a rapid rate of regression, the other curve has a slow rate of regression. There appears to be no explanation for wide differences. Low numbers of flies were recovered in both cases, however, within three miles of the release points. Lower recoveries continued from three to six miles.

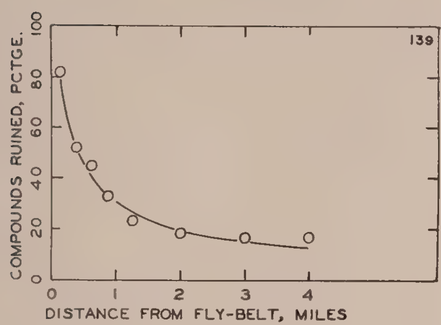

Fig. 139

Incidence of ruined compounds at distances from the fly-belt (data from Morris).

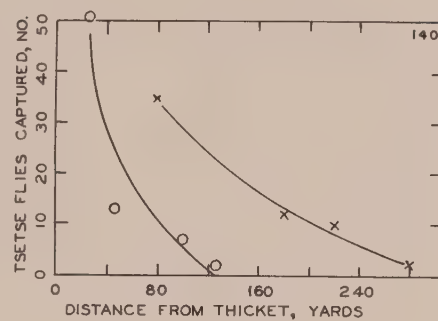

Fig. 140

Incidence of attraction of tsetse flies moving to host animals.

Curve drawn about circles represents data from the dry season.

Curve drawn about the X characters represents data from the wet season (data from Moggridge).

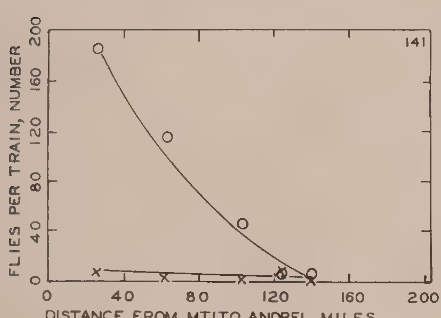

Fig. 141

Dispersion of tsetse flies on railway trains.

Upper curve represents flies caught on goods trains.

Lower curve represents flies caught on passenger trains (data from Lewis).

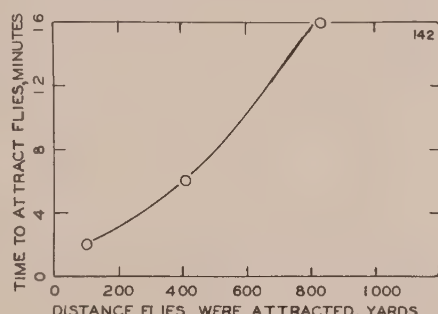

Fig. 142

Time to attract the oriental fruit fly at distances from methyl eugenol (data from Steiner).

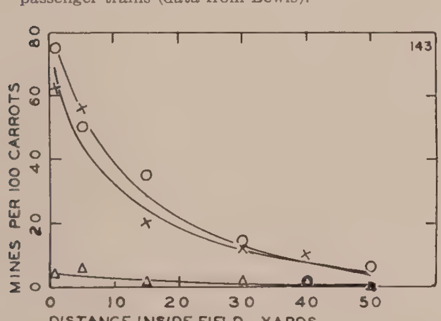

Fig. 143

Incidence of larval mines of carrot fly at distances from headlands. Different curves represent different observations (data from Wright & Ashby).

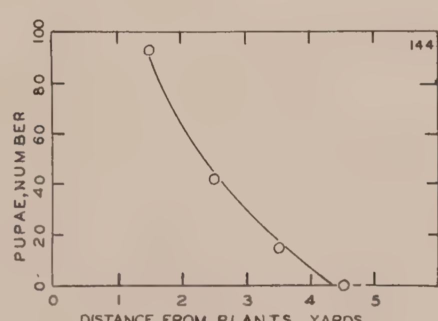

Fig. 144

Dispersion of carrot fly larvae for pupation (data from Petherbridge and Wright).

Radioisotopes were used by Schoof et al. (1952) for marking houseflies to determine dispersion. Baited fly traps were used for recapturing marked flies. A regression curve was drawn to show the rate of dispersion for flies in each of the two tests (Fig. 134). Rapid and similar rates of decrease were found for both tests over the 0.5 to 2.0 mile distance range. The June test terminated at three and the September test ended at five miles from the release sites. There is fair agreement of observed and curve values.

A total of 342,000 houseflies tagged with p^{32} given in the food were released at five sites, according to Schoof and Silverly (1954a). A different dye was used for the specimens released at each of the liberation sites. Selection of the release sites depended on possible attractiveness or lack of attractiveness to the flies according to breeding potentials. A regression curve was drawn to show the rate of dispersion from each site (Fig. 135). Tagged flies were taken at distances of nearly eight miles, the maximum distance from the release site at which traps were placed. The highest percentage of tagged flies was taken at the "Hog Farm" release site, also the regression curve suggests dispersion ended at some distance in excess of eight miles. The lowest percentages of tagged flies were taken at the "Rendering Plant" release site. All curves have similar rates of curvilinearity indicating similar rates of housefly dispersion regardless of release site characteristics.

Radioactive houseflies were released by Lindquist et al. (1951) for studies of their flight habits. A small portion, 4.6 per cent, of the released insects was recovered. A regression curve was drawn to illustrate the rate of recovery as affected by distance (Fig. 136). A very rapid rate of percentage decrease was found to about three miles, with low percentages of recoveries to eight miles from the release site. Close agreement of observed and curve values is lacking.

In dispersal studies of houseflies, *Musca domestica vicinia* Macq., Wolfinsohn (1953) fed sugar with finely divided ferric oxide to flies and put out recapture traps lined with adhesive to which flies became fast and could be examined and counted. From the data given a regression curve was drawn (Fig. 137). A rapid regression is indicated between 55 to 220 yards from the release site. A much reduced rate of regression is indicated, however, for distances between 220 and 330 yards. Fly dispersal extended to some distance in excess of 330 yards. There is very close agreement of observed and curve values.

In studying movements of populations of a tsetse-fly, *Glossina morsitans* Wst., Jackson (1940) caught, marked, and made recoveries of flies. Although special attention was directed to the movements of flies among the squares data were given to show distances to which released flies were recaptured. A regression curve was drawn from these data (Fig. 138). A distance range of about 3.5 miles is indicated for the dispersion of the male flies. Except for the recovery at ⅔ mile there is fair agreement of observed and curve values. Further reference is made to the study under Generalizations.

A climax in human endeavor is seen in the observations by Morris (1952) on the human habitation-tsetse fly-sleeping sickness cycle. Natives must have water; hence, live near a river in compounds. Tsetse flies, *Glossina morsitans* Wst., also live along the river in fly-

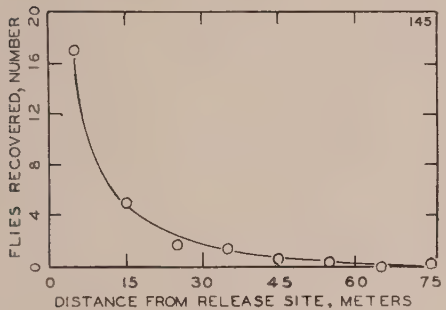

Fig. 145
Dispersion of *Drosophila funebris* from release sites (data from Timofeef-Ressovsky).

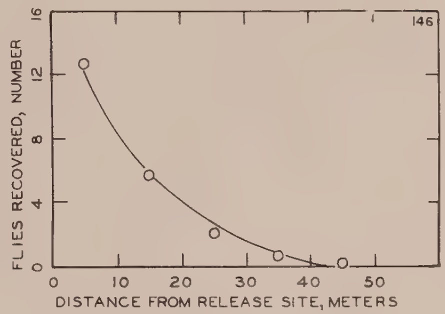

Fig. 146
Dispersion of *Drosophila melanogaster* from release sites (data from Timofeef-Ressovsky).

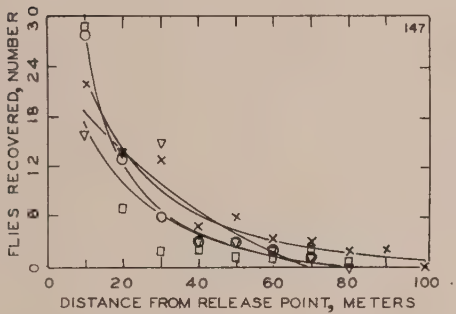

Fig. 147
Dispersion of fruit flies from release site (data from Burla, et al.).

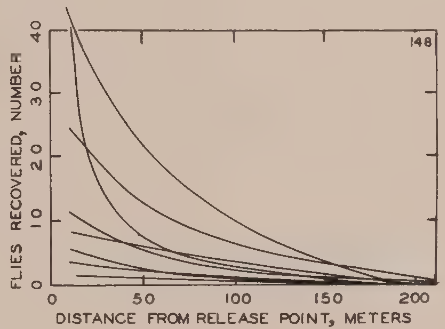

Fig. 148
Dispersion of fruit flies
Different curves represent different days collections (data from Dobzhansky and Wright. Expt. 1).

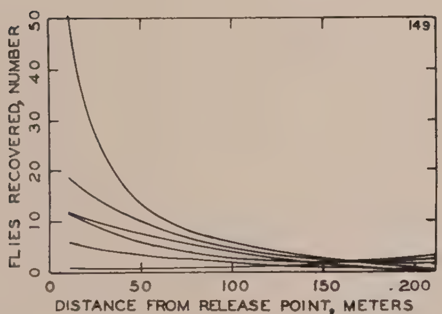

Fig. 149
Dispersion of fruit flies
Different curves represent different days collections (data from Dobzhansky and Wright. Experiment 2).

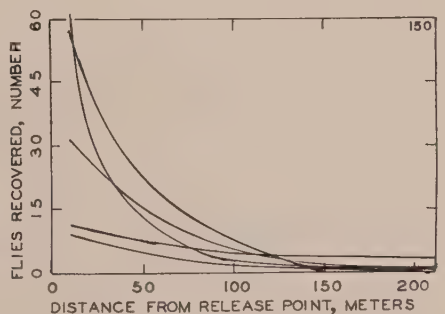

Fig. 150
Dispersion of fruit flies
Different curves represent different days collections (data from Dobzhansky and Wright. Experiment 3).

belts. Those compounds in and nearest the fly-belts suffer most from the pestilential sickness. People in many compounds perished; other people moved further from the rivers. Ruined compounds were found by Morris (1952) most frequent within a mile of fly infested areas and became less frequent with increasing distance from tsetse fly habitats. A regression curve was drawn to show depopulation as related to the nearest fly belt (Fig. 139). Low percentages of ruined compounds were found at two miles from fly belts. Between two and four miles there was little slope to the regression curve. There was no change in the observed percentages of ruined compounds. Zero percentage of ruined compounds was reached at some distance in excess of four miles.

Tsetse flies, *Glossina palpides* Newst., are attracted from thickets to host animals moving in open areas as shown by Moggridge (1949). More flies are attracted to target animals nearer the thickets than at more remote distances. Two regression curves were drawn to show attractiveness in the dry season (Fig. 140). Two very different regression curves are recognized. Seasons evidently influence conditions that attract tsetse flies. Few flies were captured at 120 yards from thickets in a dry season. Few flies were captured at 280 yards in a wet season. The curve illustrative of fly abundance in the dry season is the steeper curve, indicating less effect of distance in dry than in the wet season. There is fair agreement of observed and curve values.

Considerable agitation for quarantine is sometimes made with reference to "hitch hiking" insects, i. e., those which are dispersed by automobiles, ships, airplanes, trains or other modes of transportation. Although there is no question but that insects are dispersed by man or by man's agents there are questions concerning the frequency, amount and distances traveled by such organisms.

In tsetse fly studies in the Kenya Colony, Lewis (1950) procured data on transportation of the flies by railway trains. Although *Glossina longipennis* Corti was the most abundant species caught other species taken were *G. pallidipes* Aust., *G. brevipalpus* Newst., and *G. austeni* Newst. More flies were taken in the fly belt and fewer toward the coast. Two regression curves were drawn, one for passenger trains and one for goods trains (Fig. 141). Extremely wide differences were found between kinds of trains as to the number of flies per train. Goods trains carried many more flies than passenger trains. A rapid decrease was found in numbers of flies on goods trains to about 140 miles from Mtito Andrei (taken as the source of the flies). A low number of flies was always found on passenger trains.

Trypetidae.—Response to the fruit fly attractant methyl eugenol was more rapid at short distances than at more remote distances according to Steiner (1952) for the oriental fruit fly *Dacus dorsalis* Hendel. Observed values on the time to reach the attractant from the distance attracted were used for drawing a regression curve (Fig. 142). Flies were attracted from as much as 800 yards from the attractant at an average speed of 54 yards per minute. Although logarithmic conversions of time and distance were used for computing the regression curve further work is needed to determine the relationships of the activities involved in this phase of insect dispersion. Dispersion was by flight.

Psilidae.—Shelter in uncultivated headlands provided protection for the carrot rust fly, *Psilia rosae* F., in such manner that carrots were mined more extensively nearer the field margin. Effects of adjacent shelter on carrot fly infestations were given in the report by Wright and Ashby (1946). Three curves were drawn from the data and are given in Fig. 143. Low infestations were reached at near 50 yards inside the field. Two curves are similar in slope and in position. The third curve drawn from data taken in another field indicated a low infestation existed, even near the field margin.

Carrot rust fly, *Psilia rosae* F., larvae pupate in the soil around the host plants after they have attained maturity. Distances to which these larvae disperse for pupation were given by Petherbridge and Wright (1943). A regression curve was drawn to show distances to which mature larvae moved for pupation (Fig. 144). Most pupae were found between one and two yards from the plants. No pupa was found in excess of four yards. There is fair agreement of observed and curve values. Dispersion was accomplished by burrowing in the soil.

Drosophilidae.—One of the first release-recapture experiments on *Drosophila* was conducted by the Timofeeff-Ressovskys (1940a). Specimens were marked and released for recapture at food traps. From figures given by these authors (1940b) on *Drosophila funebris* (F.) a regression curve was drawn (Fig. 145). A steady reduction was found in the number of flies recaptured at distances to 45 meters from the release site. There is close agreement of observed and curve values.

Records on the number of marked, released and recaptured specimens of *Drosophila melanogaster* Meig. were given by Timofeeff-Ressovsky (1940b). Recapture stations at 10 meter intervals about the release site took few released insects from two lots of specimens but a much greater portion of a third lot. From the data given, a regression curve was drawn (Fig. 146). Recovered specimens were taken to distances of 75 meters although most recaptured insects were taken within 25 meters of the release site. There is fair agreement of curve and observed values.

Four experiments were conducted by Burla et al. (1950) on dispersion studies of the hairless mutant of *Drosophila willistoni* Sturtevant. One or more days after the insects were released baits were placed at various distances from the release site for collecting flies. Between 4154 and 5505 flies were released for each experiment. A regression curve was drawn to show the rate of dispersion for each experiment (Fig. 147). Curve positions and curvilinearities are similar for each experiment. There are some differences, however, part of which may be attributed to temperatures existing at the time the experiments were conducted. Low frequencies of recovered flies were obtained at near 80 meters from the release site.

Extensive studies were made by Dobzhansky and Wright (1943) to determine the rates of dispersion of *Drosophila pseudoobscura* Frowola. These show the marked effects of distances to 500 meters from the release point. Daily collections of released specimens attracted to baits show day-to-day rates of dispersion. Four experiments were conducted during the summer months of June and July. Regression

curves were drawn for the daily collections for each experiment. Data from five to eight of the daily collections of each experiment were used for drawing the regression curves. After five to eight days the collections were so few that the data were not used. In Figs. 148, 149, 150 and 151 no observed value is indicated owing to the mass of observations and the confusion that might arise. In general the topmost curve, also the one having the most slope represents the first days collection of released flies. The lowest curve and also the one having the least slope represents the collection made on the last day. Curves drawn from the four experiments are given in Figs. 148, 149, 150, and 151. Low incidences of recovered flies were reached at near 150 meters from the release site in all experiments. Recoveries were made, however, to 200 meters. In consideration of the regression curves dispersion of the flies extended to distances in excess of 200 meters. Further references are made to these studies under Generalizations.

Orange-eyed *Drosophila pseudoobscura* Frolowa were released by Dobzhansky and Wright (1947) to interbreed with wild flies for studying the rate of dispersion of a mutant gene through the wild population. Ratios of orange-eyed to wild flies were used instead of numbers to obviate, ". . . in part the complications due to varying densities of the fly populations and variable numbers of traps in different parts of the experimental field." Ratios were obtained at three distance points, "point of release" (assumed as of 1 meter), 500 and 1000 meters. Two curves were drawn to summarize the results (Fig. 152). Ratios of orange-eyed to wild characters were higher nearer the release point than at more remote distances. Both curves reached low levels within 1000 meters of the release point. There is close agreement of observed and curve values.

Interbreeding of orange-eyed and wild flies resulted in heterozygous individuals so that after a time it became necessary for Dobzhansky and Wright (1947) to make breeding tests to determine presence of the orange-eyed gene. Ratios were also used to express these data which were obtained by sampling two and one-half and 11 months after release of the orange-eyed stock as shown in Fig. 153. A higher ratio was found nearer the release site than at more remote distances for each sampling period. There was chromosomal dispersion, however, to distances in excess of 100 meters from the release point. Lower ratios of orange-eyed to wild gene-bearing flies were found at the 11-month sampling period than at the two and one-half month period. This is indicative of gene diffusion through a wild population but that it was a recessive character and soon began to disappear.

Radioactively tagged drosophilids were released by Pimental and Fay (1955) in pit privies to study the dispersion. Collections were taken by traps placed in residences and in pit privies. Data from collections of *Drosophila repleta* Woll., were pooled from traps in residences and in pit privies for drawing a regression curve (Fig. 154). A rapid rate of regression was found to about 150 feet followed by a less rapid rate to near 600 feet. There is fair agreement of observed and curve values.

Agromyzidae.—More leaf mines per leaf made by the serpentine leaf miner, *Liriomyza pusilla* Meig., were present in potato leaves nearer

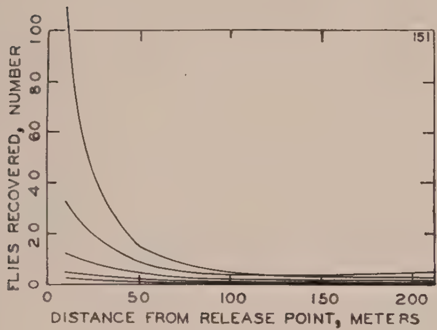

Fig. 151

Dispersion of fruit flies

Different curves represent different days collections (data from Dobzhansky and Wright. Experiment 4).

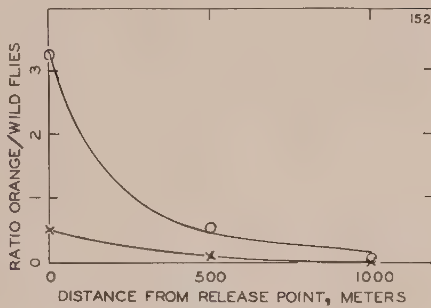

Fig. 152

Incidence of chromosomal invasion of orange-eyed in a wild population of *Drosophila* flies.

Upper curve represents data taken two weeks after release of flies.

Lower curve represents data taken four weeks after release of flies (data from Dobzhansky and Wright).

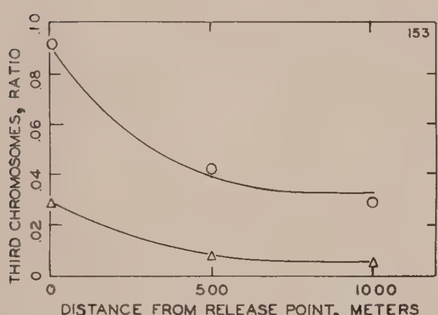

Fig. 153

Incidence of chromosomal invasion of orange-eyed in a wild population of *Drosophila* flies.

Upper curve represents data taken two and one-half months after release.

Lower curve represents data taken eleven months after release of flies (data from Dobzhansky and Wright).

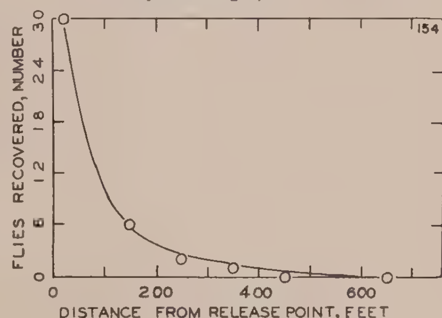

Fig. 154

Dispersion of *Drosophila repleta* flies (data from Pimental and Fay).

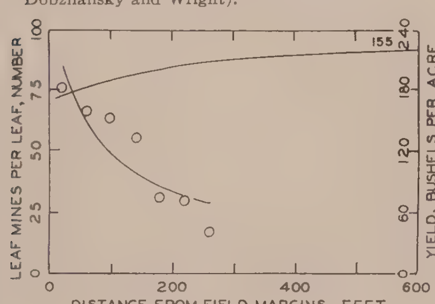

Fig. 155

Incidence of leaf mines in leaves and of yields of potatoes at distances from field margins.

Downward curve represents leaf mines.

Upward curve represents yields (data from Wolfenbarger).

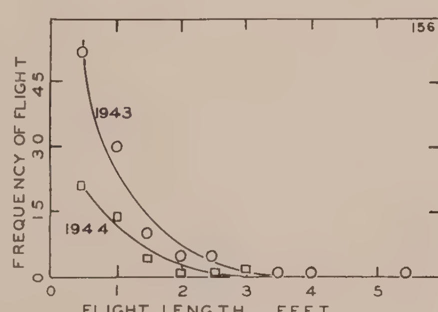

Fig. 156

Flight lengths of solitary bees foraging among turnip blooms (data from Bateman).

field margins than in the central portions, and potato yields were higher per unit area in rows more distant than in or near the field margins, according to Wolfenbarger (1948). Two regression curves were drawn, one is given to show the relative numbers of leaf mines, the other is given to show the yield as related to the field margin (Fig. 155). A rapid rate of regression of leaf mines is shown in which much reduction was observed within 250 feet. A lesser rate of regression, however, shows yield reductions to a distance of about 300 feet after which there are lessened increases to 600 feet from the field border. There is poor agreement of observed and curve values pertaining to leaf mines. Although a semi-logarithmic transformation was used the observed values suggest a linear relationship by untransformed values.

Andrenidae.—Solitary bees, *Andrena* sp., were observed by Bateman (1947c), in studies on contamination of seed crops, to fly short distances in visiting turnip blooms. From the data given two regression curves were drawn (Fig. 156). Low frequencies of flight lengths were reached one year, 1943, at near three and one-half feet, and the other year, 1944, at near three feet. Although the curvilinearities of the curves are similar the positions are somewhat different.

Bombidae.—Flight lengths of bumble bees foraging on radish bloom were usually less than two feet according to Bateman (1947c). A regression curve was drawn to show the frequency of distances to which the bumblebees flew between blossoms (Fig. 157). The distance traveled by the bumblebees in going from flower to flower was usually less than two feet. Rarely did the insects cover distances in excess of four feet.

Apidae.—Flight lengths of hover flies, solitary bees and bumblebees as they foraged were measured and are given above. Data were also given by Bateman (1947c) on the distance between visits measured for honeybees, *Apis mellifera* L., as they foraged turnip bloom. Observations were made for two seasons on honeybees and solitary bees and one year on bumblebees and hover flies. Two regression curves were drawn to show flight lengths of the honeybee; one to show the data taken 1943, and the other to show the data taken in 1944 (Fig. 158). Most flights were less than two feet in length. Flights were longer in 1943 than in 1944. The regression curve reached zero at near six feet for the 1944 data, whereas the curve reached zero at near three feet for the 1944 data. Similar curvilinearity is displayed by both regression curves although the positions of the curves indicate two different populations. Abundance of blossoms per unit area, nectar per blossom, wind speeds, or lurking enemies are suggested as factors causative of different flight lengths. There is fair agreement of observed and curve values.

Five minute counts of returning honeybees made near sunset, show that successively fewer insects return with the approach of darkness. The data given by Ribbands (1951) show, too, that fewer insects return from more distant than from nearby crop plants. Three regression curves were drawn to show the results (Fig. 159). Effects of distance from nectar producing plants were marked in that honeybees returned later from nearby crop plants than from plants 0.375 or 0.750 miles distant. Later evening flights were initiated to return to

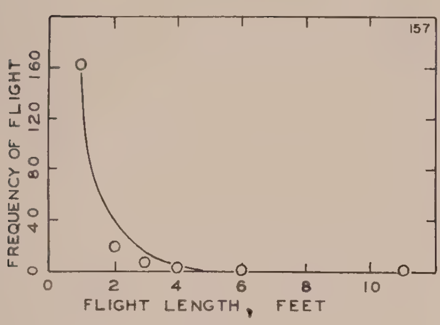

Fig. 157

Flight lengths of bumble bees foraging among radish blooms (data from Bateman).

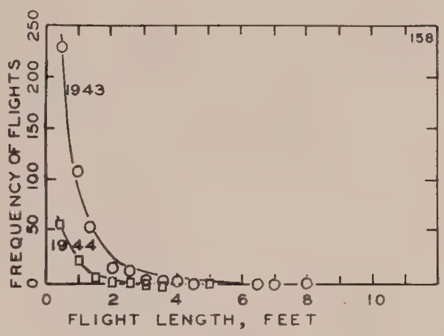

Fig. 158

Flight lengths of honeybees foraging among turnip blooms (data from Bateman).

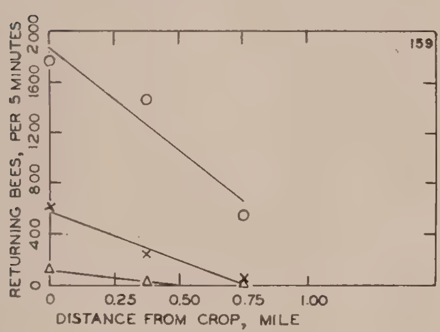

Fig. 159

Incidence of returning honeybees from crop plants.

Upper curve represents insects returning after 8:30 P. M.

Middle curve represents insects returning after 8:45 P. M.

Lower curve represents insects returning at 9:00 P. M. (data from Ribbands).

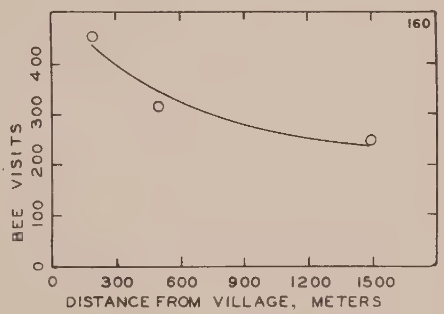

Fig. 160

Honeybee visitations at distances from apiaries (data from Kratochvil, et al.).

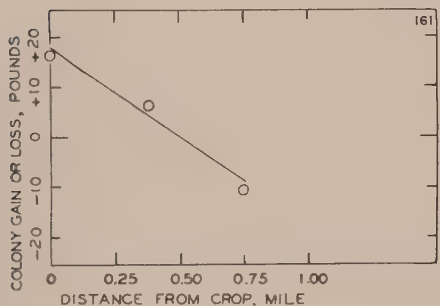

Fig. 161

Gain or loss in weight of honeybee colonies at distances from apple trees (data from Ribbands).

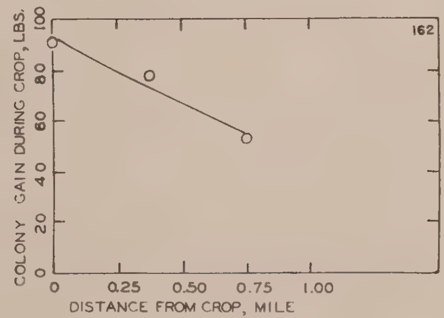

Fig. 162

Honeybee colony gain in weight at distances from lime (European linden) plants (data from Ribbands).

the colony site nearer to the plants than at more remote distances. Although untransformed data were used for computing the curve values, these are given as tendencies. Later observations may show that the honeybee activities involved may function as a straight line.

Honeybee visits to red clover, *Trifolium pratense* L., were most frequent nearest the villages, where the apiaries are located, according to Kratochvil et al. (1948). Pollination was also influenced as a result of bee visitations. A regression curve was drawn to show the comparative visitations (Fig. 160). Visitations were about one-half as frequent at 1500 as at 200 meters from the villages. There was a gradual reduction in visitations over the distance range covered. Fair agreement exists between observed and curve values.

Gain or loss in weight of honeybee colonies at distances from crop plants was the subject of studies by Ribbands (1951) covering results of two years. A regression curve was drawn to show the results of gain or loss at distances from apple trees (Fig. 161). Zero weight gain was reached at about one-half mile from the apple trees. There is fair agreement of observed and curve values. Untransformed data were used for computing the regression. This may be evidence that gains in colony weights, owing possibly to out-going and return flights, function as regular (untransformed) data.

Gains in weight on honeybee colonies from lime trees (European linden) were obtained by Ribbands (1951) to distances of three-fourths mile from the crop. Although more gains in weight were made in 1949 than in 1950 the data from the two years were pooled for drawing a regression curve (Fig. 162). Distances affected the colony gain very markedly. As observed in Fig. 162 one mile may be expected to reduce the gain in weight by about one-half. Part of the reduction is attributed to increased flying time between the plants and the hive.

Honeybee abundance as measured by the number per two square yard areas was given by MacVicar (1952) in studies on red clover, *Trifolium pratense* L., seed production. A curve was drawn to illustrate the trend among the observed values (Fig. 163). Only a very slight reduction was found in the comparative numbers of honeybees over the distance range covered. Close agreement of observed and curve values is lacking.

A unique feature of the work reported by Braun et al. (1953) is the nectar concentration (per cent solids) and volume of nectar per floret in red clover at distances from the apiary. The per floret concentration decreased and the volume increased with distance from the apiary. Two regression curves were drawn to show the results (Fig. 164). Concentration of the nectar varied significantly with the distance. Although volume of nectar per floret was greater with distance increase the differences were not significantly so. It is suggested that foraging honeybees, present in greater abundance nearest the apiary kept more of the nectar gathered from the nearest florets whereas it accumulated in the florets at the greater distances. Dispersion of the Apidae was by flight.

Data on red clover, *Trifolium pratense* L., seed production and honeybee abundance per two square yard area were determined by Braun et al. (1953) over a distance range of 130 to 2330 feet from the

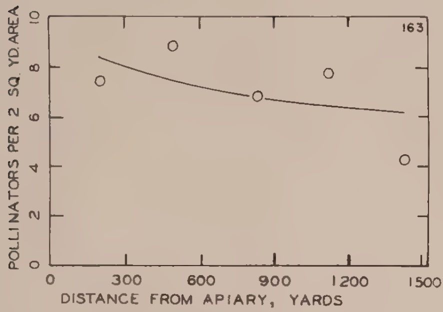

Fig. 163

Incidence of pollinating insects at distances from an apiary (data from MacVicar, et al.).

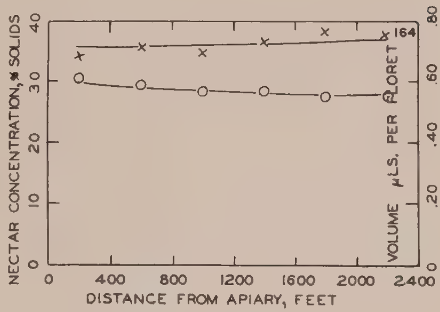

Fig. 164

Incidence of percentage solids and volume of nectar per floret at distances from an apiary.

Upper curve represents volume of nectar per floret.

Lower curve represents concentration of solids (data from Braun, et al.).

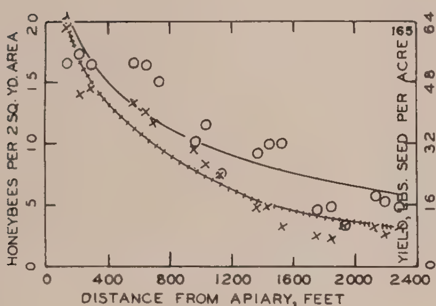

Fig. 165

Incidences of honeybees per unit area and of yield of red clover seed at distances from an apiary.

Solid line represents the number of honeybees per unit area.

Barred line represents the yield of red clover seed (data from Braun, et al.)

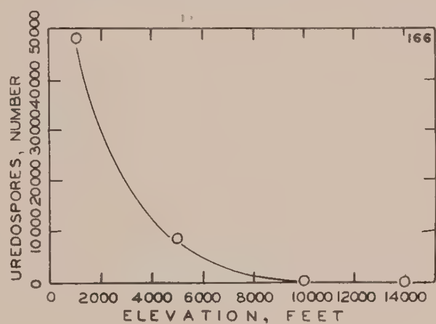

Fig. 166

Vertical dispersion of uredospores of wheat stem rust (data from Craigie).

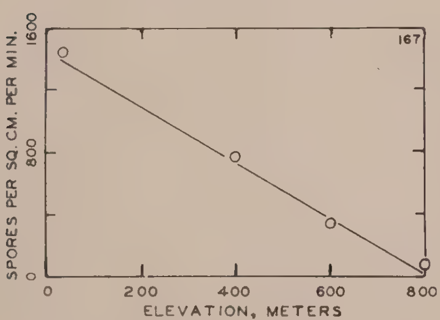

Fig. 167

Vertical dispersion of spores of wheat stem rust (data from Hubert).

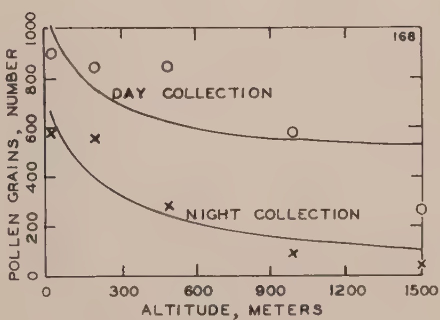

Fig. 168

Vertical dispersion of pollen grains (data from Rempe).

apiary. A regression curve was drawn to show seed production and honeybee abundance (Fig. 165). Red clover seed yield was approximately eight-fold greater at the 130 than at the 2330 foot distance, according to the regression curve. Honeybees, however, were but about four-fold greater at 130 than at the 2330 foot distance. The regression curve representing honeybee abundance is more flattened than the curve representing seed yield. This indicates seed production was more responsive to the distance range than was honeybee distribution. Although close agreement of observed and curve values is lacking the authors found significant differences in honeybee populations at different distances.

VERTICAL DISPERSION

Data on elevations to which organisms disperse or are dispersed are given by various authors. These data are suggestive that distant horizontal dispersion may occur if organisms are taken at high altitudes. Data which show that organisms remain at low elevations are suggestive of dispersion over ranges having short distances. A relationship may exist between organisms which disperse high vertically and distant horizontally as contrasted with those which disperse to low elevations and to short distances horizontally. Vertical and horizontal dispersions were recognized by Gregory (1945) as part of the same dispersion process. Of the many organisms beginning the process, it is the living, viable organisms that arrive which are of significance. Vertical distances are necessary and serve dispersing organisms as needed. Insects in utilizing heights to avoid obstructions meet the purpose reported by Osborne (1951) and fly at low elevations thus economizing energy and avoiding loss of life.

Uredospores of wheat rust, *Puccinia graminis* Pers., from the collections of two days, August 5 and 10, 1930, as reported by Craigie (1945) were pooled for drawing a regression curve. Comparative numbers of spores per square inch were taken to elevations of 14,000 feet and were used for drawing a regression curve (Fig. 166). At 100 feet elevation 48,200 uredospores were comparable with 144 and 40 at 10,000 and 14,000 feet, respectively. Reductions in spores collected became much less above 8,000 feet. There is fair agreement of observed and curve values. Air currents were the agents of dispersion.

During a yellow rust, *Puccinia glumarum* (Schmidt) Erikss. & Henn., epidemic of wheat near Halle, Germany, Hubert (1934) reported on two airplane flights for trapping rust spores. From data given, it was found that a straight-line relationship of vertical height with number of spores trapped existed where untransformed values were used. The results are shown in Fig. 167. A regular and steady decline was found in the number of yellow rust spores with increases in height to 800 meters. There is very close agreement of observed and curve values.

Various species of pollen grains were trapped at different elevations as reported by Rempe (1937). Data were obtained by day and night-time flights. From these data two regression curves were drawn (Fig. 168). Day-time collections took more pollen grains than night-time collections. Comparatively fewer pollen grains were taken at higher

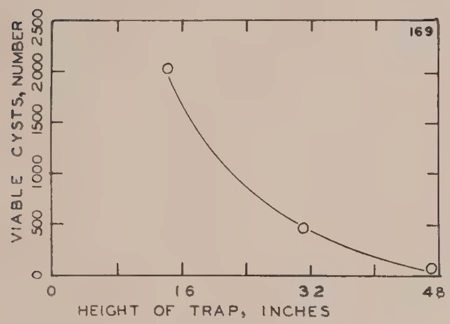

Fig. 169
Vertical dispersion of potato root eelworms (data from White).

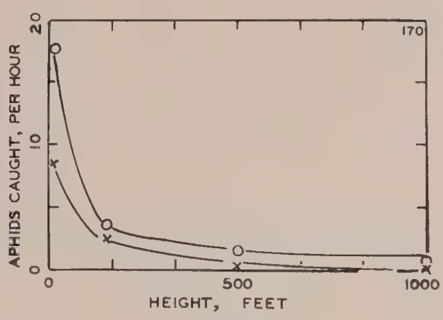

Fig. 170
Vertical dispersion of aphids
Upper curve represents a seven-hour collection period.
Lower curve represents a 65-hour collection period (data from Johnson and Penman).

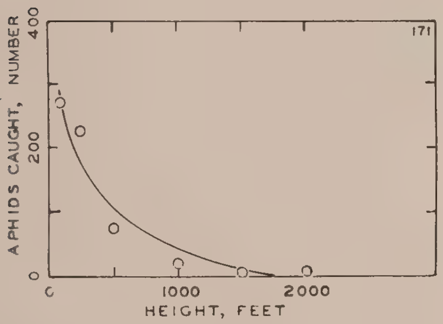

Fig. 171
Vertical dispersion of aphids (data from Johnson).

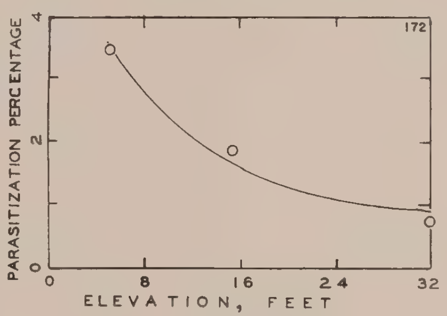

Fig. 172
Vertical dispersion of parasitized sugar-beet leafhoppers (data from Lawson, et al.).

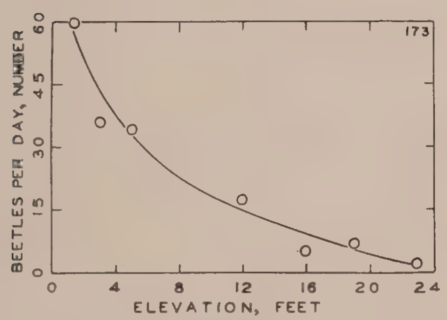

Fig. 173
Vertical dispersion of the tobacco flea beetle (data from Dominick).

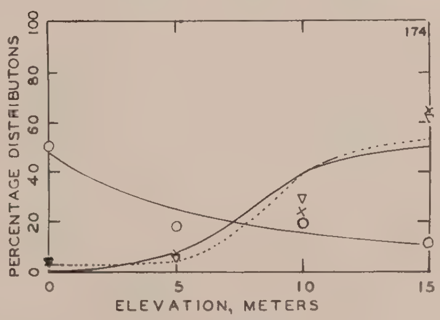

Fig. 174
Vertical distribution of mosquitoes in a forest.
Solid line curving downward represents *Anopheles darlingi.*
Solid line curving upward represents *A. mediopunctatus.*
Dotted line represents *A. shannoni* (data from Deane, et al.).

elevations by night than by day-time flights, according to the curves. Observed and curve values lack close agreement. Although it may be questioned that regular untransformed data might provide closer alignment the elevations were transformed to logarithmic values for computing the regression.

Vertical dispersion of the potato-root eelworm, *Heterodera rostochinensis* Woll., were observed by White (1953). Fully viable cysts were borne by wind currents to elevations of four feet (Fig. 169). Rapid reductions were found from near 16 to 48 inches in elevation. Extrapolation of the curve to elevations of less than 16 inches suggests much vertical dispersion. There is close agreement of observed and curve values.

Density of aphids was related to altitude as shown by Johnson and Penman (1951). In their early studies tow nets were used for making collections. They began using suction traps, however, in 1950, and considered this method of collecting aphids was the more reliable. Two curves were drawn from the data given, one for 65 hourly occasions, the other for seven hours (Fig. 170). Aphids were collected at all heights but their abundances decreased rapidly as heights increased. Transformations of the data to logarithms were made by the authors to show the relationships. Fair agreement of observed and curve values was found, however, by calculating curve values by the modified semi-logarithmic formula.

Tow nets were used by Johnson (1951) for collecting insects although defects in earlier methods of calculating densities were recognized. Data on collections taken by day and night trapping were pooled for calculating a regression curve (Fig. 171). Zero aphid collection was reached according to the regression curve at near 1700 feet elevation. This compares with a curve value of 292 aphids at 50 feet elevation.

Parasitized individuals of the sugar beet leafhopper, *Circulifer tenellus* (Baker), were found by Lawson et al. (1951) to fly at lower altitudes than the non-parasitized individuals (Fig. 172). Nearly five times as many parasitized leafhoppers were found at 2.5 feet elevation as at 32.0 feet.

Gravid females of the sugar beet leafhopper, *Circulifer tenellus* (Baker), fly under some conditions but are generally less active than females with undeveloped eggs. Data on the abundances of gravid females at three elevations were given by Lawson et al. (1951). These data for which no regression curve was drawn are given as follows:

Elevation, feet	2.5	15.0	32.5
Gravid females, percentage	7.4	8.1	4.6

Since there were more insects at the 15.0 foot elevation that at 2.5 or 32.5 foot elevation, it is not certain which form a regression curve might take. It is suggested, however, that 2.5 feet is so near the ground level insects fly higher to avoid obstructions. The 32.5 foot elevation may be higher than is necessary to avoid obstructions, while the 15.0 foot elevation is high enough to avoid obstructions and low enough to avoid buffetings of winds at higher elevations.

In studies on the life history of the tobacco flea beetle, *Epitrix parvula* (F.), Dominick (1943) found the insect flew in greater abun-

dance nearer ground level. Data for the week of September 9–16 on number of beetles taken at different heights were used for drawing a regression curve (Fig. 173). Diminishing numbers of beetles extended from 1.5 to 23.0 feet elevation. In part of the data, however, more beetles were taken at 2–4 than at 1–2 feet elevation. This tendency was more prevalent in the earlier than in the later part of the season. There is fair agreement of observed and curve values.

Studies of vertical distribution of mosquitoes in a forest by Dean et al. (1953) showed that of three species two, *Anopheles shannoni* Davis and *A. mediopunctatus* (Theo.), were more abundant at 15 meters than at lower elevations. A third species, *A. darlingi* Root, however, was more abundant at ground level and became less abundant with increased elevation. Three curves were drawn, one for each species, to show the relationships of elevation and relative abundances (Fig. 174). Gradual decreases in abundance of *Anopheles darlingi* were shown with increases in elevation. Gradual increases in mosquito abundance with elevation increases, however, were found with *A. shannoni* Davis and *A. mediopunctatus* (Theo.). Such increases cannot proceed indefinitely but must cease after which decreases in abundance with increases in elevation must occur. The regression curves suggest a peak of abundance near the 15 meter elevation.

Generalizations, Part 2

All organisms originate with the parent and through enlargement, growth, and maturation must make a separation from it. This separation initiates a disperse phase which is common for all organisms, according to Andrewartha and Birch (1954). All organisms, moreover, are prepared and ready at one or more stages for dispersing or of being dispersed. The disperse phases embrace greater or lesser distances as is indicated in Part 1. The young of most species are concentrated on small areas where nativity occurs. The concentrations are observed and recognized, for example, as spores in fungus fruiting bodies, pollen and seed in plants and insects in egg masses. It is evident and necessary that an exodus be made from such concentrations. Growth and maturation lead to separation from the parent by the offspring of passively dispersed organisms, occasionally aided by some agent such as water, insects or wind currents. Growth and maturation of the offspring of active disperser organisms give rise to responses and actions that become propulsion and motion.

Dispersion of fungus spores is a mechanistic process, as viewed by Gregory (1952). Dispersion of insects is considered instinctive; that of a lepidopteran, *Colias*, is mechanistic, according to Smith et al. (1949).

Sufficient space for development and reproduction is a requirement for individuals of all races. Factors that bring about the accomplishment of density patterns observed in final distributions may be operative during the dispersal process, especially with active disperser organisms. Members of a race tend to grouping or irregular arrangement patterns whether of plant or animal life. The term "random dispersal" as sometimes used may imply aimless wandering, equal spacing of individuals, or an absence of cause or purpose in dispersal. Unequal

abundance, or grouping, has been discussed by Ashby (1948), Beall and Rescia (1953), Dice (1952), and Goodall (1952). Terms such as "over dispersion", "under dispersion", "aggregation" and "contagious distribution" have been applied to grouping or the unequal distribution of organisms. In view of the nonrandom distributions of members of a species in a population various studies have been made to determine the formation of arrangement patterns. A measure of spacing between individuals was discussed by Dice (1952), in which a procedure was proposed for the measurement of distances from each individual to its nearest neighbor to determine definite areas of occupation. A simplification of the procedure was given by Clark and Evans (1954) for measuring spatial relationships.

Generalizations on agencies and means of dispersion were discussed earlier, Wolfenbarger (1946), and are omitted from this paper.

Dispersion is usually accomplished by the younger and more immature stages of a species. Enemies and other factors limiting to life are probably more unfavorable to species during the disperse phase than at other times. Many or even most dispersing organisms are lost before they have reproduced their kind. The term "wastage" was used by Stakman (1946) in reference to spores and by Lloyd (1936) in reference to tsetse flies. Mortality and dilution of dispersive populations combine to reduce populations of organisms as they emanate from the origin.

ACHIEVEMENTS OF DISPERSION

Dispersion is one of the processes by which the needs or demands of an organism are achieved. Two of these objectives achieved by dispersion are mating and maintenance of the individual. Another objective (although not recognized as such by the organism) is for extension of the species into areas not previously inhabited. A final classification is Miscellaneous Achievements. The accomplishments of dispersion include reproduction of the race, spread of newly developed characters, reduction of inbreeding and the promotion of the stabilization of racial characters.

Food and Shelter.—Organisms usually compete with others to obtain food and shelter. Although most organisms live among others of their race and near to or with other species a thinning process is necessary to obtain the necessities of life. Further discussions pertaining to the subject of distribution are numerous but comments on interspecific association, population interspersion, plant distribution, interspecies competition and interactions are given by Cole (1949), Elton (1949), Goodall (1952), Park (1948), Ashby (1948) and Thompson (1939), respectively.

Most organisms originate in areas and under conditions favorable for the species to obtain food and shelter. Favorable conditions for the parents in an environment are generally favorable for their progeny and such conditions tend to remain favorable for continued repopulation.

Distances of dispersal for food and shelter are undoubtedly greater than for most other purposes. Much depends on the species involved and on the purposes compared. Although various life activities require dispersal distances for different phases or stages of development dis-

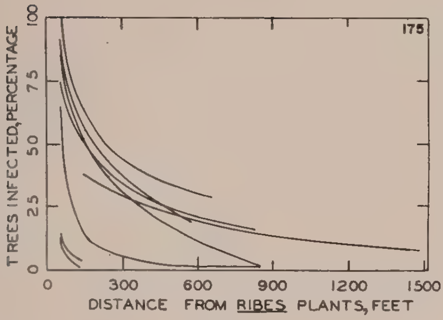

Fig. 175
Incidence of white pine blister rust (data from various authors).

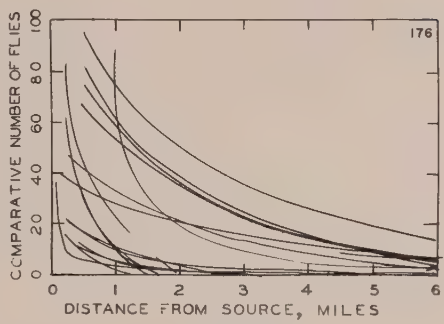

Fig. 176
Dispersion of the housefly (data from various authors).

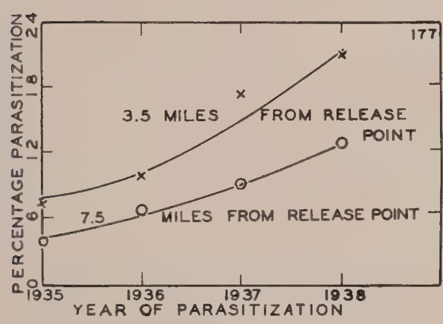

Fig. 177
Incidence of parasitization annually and at two distances from the release site (data from Baker, et al.).

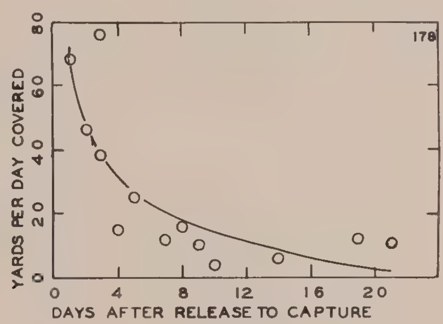

Fig. 178
Dispersion of *Aedes albopictus* as affected by age (data from Bonnet and Worcester).

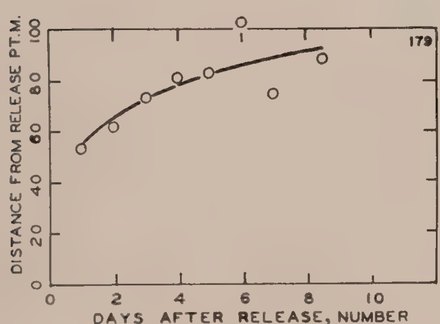

Fig. 179
Regression of distance on days after release of drosophilids (data from Dobzhansky and Wright).

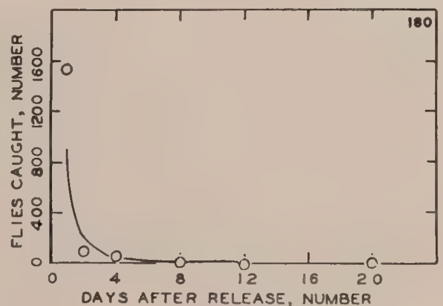

Fig. 180
Recovery of houseflies on days after release (data from Lindquist, et al.).

persal for the procurement of food and shelter remain prominent and paramount activities.

Invasion of Unoccupied Areas.—Attempts are made repeatedly by individuals of a species to invade and attempt the occupation of areas new to it. This was termed "extra-limital" distribution by Brown (1950). Races sometimes result from genetic variations that succeed in areas new to a species.

Those individuals entering territory new to the race may encounter enemies and frequently more adverse living conditions. Limiting factors or barriers destroy or prevent many of the invading individuals from reproduction. Those organisms entering new areas are more likely, therefore, to be lost to the race than are those which settle near the origin. If, however, organisms enter a new area and become established the race may be more fruitfully abundant.

Dispersing organisms encounter barriers which range from those that are totally to those that are partially effective. Dispersing populations of organisms are restrained by variously direct and indirect means as discussed below. Physical barriers such as mountains and oceans are prominent. There are barriers restricting dispersion such as those given by Woodbury (1954) and recognized as climatic, biological, physiological and reproductive. Many of these, to the viewpoint of man, are inconspicuous and unimportant. There may be barriers unrecognized by man.

Mating.—Dispersal as a distinct activity for the purpose of mating occupies more or less conspicuous activities with most small organisms. Some plants are recognized as functioning hemaphroditically, however, and some insects reproduce for many generations or even permanently by parthenogenesis, without intervention of males. Pollen dispersal is an important example of mating in plant life and it is frequently very conspicuous, although for but a short season each year. Males of the gypsy moth, *Porthetria dispar* (L.), were found by Collins and Potts (1932) to disperse upward to two miles seeking the wingless female of the species.

Miscellaneous Purposes.—Small organisms exhibit various and purposeful objectives for dispersion. Larvae of many species crawl or burrow for some distance (in terms of inches or sometimes feet) seeking a site for pupation. Flights to woodlands or other areas for hibernation at distances from peach orchards by the plum curculio, *Conotrachelus nenuphar* (Herbst.) and from cotton fields by the cotton boll weevil, *Anthonomous grandis* Boh., are examples of activities of a miscellaneous character. Aside from flights for food the grape berry moth, *Clysia ambiguella* Hubn., and *Polychrosis botrana* (Schiff.) there were flights for mating, oviposition and swarming according to Gotz (1941). The honeybee *Apis mellifera* L. has several activities in which flight serves different purposes. Orientation flights are made by workers in which short distances (a few yards or several rods) are covered before they return to the colony. Such flights are made preceeding the assumption of field activities. Forage flights of honeybees, solitary bees, hover flies and bumble bees were measured by Bateman (1947a). Although homing flights of the honeybee were mentioned by Bateman (1947a) these would constitute the return part

of a field trip flight. The swarm of the honeybee might be termed a true migration since it is a group movement to a permanent abode for the reproduction of the race with the possibility of a return trip by progeny of the swarm queen. Although the queen and drone bees fly with a swarm theirs is the only true mating flight of the honeybee.

SAMPLING OR MEASUREMENT OF DISPERSION

Measurements of distance in relation to organisms dispersed and incidence of viruses and pollen given in Part 1 were obtained from sampling procedures. The samples, small portions of the entire population, were observed in order to obtain estimates of individuals in dispersing populations. Owing to the diversity of forms, habits and living places various methods and devices were used by various authors for sampling procedures.

Sampling procedures for fungus spores, pollen, and seed were discussed by Gregory (1945, 1951) Stephens and Finkner (1953) and Wright (1952). Methods of sampling insect density in the air were discussed by Bailey (1952), Glick (1939), Johnson, (1950), Johnson and Taylor (1955) and Taylor (1951).

Methods and Procedures.—Sampling procedures have often been simply and even crudely conducted. Investigators surveyed the conditions, accepted the situations involved and strove to meet the objectives sought with the equipment and materials available. Many workers have overcome handicaps and made mistakes but have made many valuable contributions. One of the most important problems encountered appears to have been that concerning the collection of positive units at the more remote distances from the site of origination of the organisms. This problem appears to ramify so many reports, although it is very often indirectly implied, that it must have been a source of frustration to many workers and there appears to be no simple solution to it. It is suggested, however, that by making many more observations at more remote distances one may expect to discover more positive units for comparison with nearby distances. There have have been improvements, however, in marking organisms and in sampling the air for members of dispersing populations.

Similarities and Variations in Regression Curves.—Two outstanding and important characteristic tendencies of regression curves depicting dispersion and incidence of small organisms are (1) a rapid initial decrease followed by less rapid decreases to low levels, and (2) low levels receding to still lower levels which approach but reach zero at remote or unknown distances. There are, however, differences in individual curves. Some curves exhibit rapid initial decreases that continue and apparently reach zero very quickly. Some curves exhibit little slope and lack of definite tendencies to reach zero. Most curves however, exhibit rapid initial decreases then assume a gentle slope and terminate without reaching zero. Data were used for drawing some curves which the authors implicitly admitted were meager or insufficient. Some of these curves and also some others were obviously drawn from insufficient data. In spite of the insufficiency, however, most curves show tendencies and possess value.

Assessments of the observations of each author's data by statistical tests of significance were not attempted.

There is some similarity among species as to distances traversed, and there is also evidence indicative of considerable variation within species. Several factors, discussed below, affect distances to which organisms disperse and introduce variations within species. There is a tendency, however, for members of a single species and sometimes closely related species to assume similar dispersion patterns.

More studies have probably been reported on the incidence of white pine blister rust, *Cronartium ribicola* F. von Wald., than on any other disease, the causative factor of which is a passive disperser organism. A reproduction of eight regression curves, (Fig. 175), show that regardless of investigator, locality or other factor, the incidences of white pine blister rust tended to similar curvilinearity. The incidence range of white pine blister rust is in terms of hundreds of feet from *Ribes* plants.

More data are available from authors on dispersion-distance effects of the housefly, *Musca domestica* L., than on any other active disperser organism. A reproduction of all or part of 17 curves is given for comparisons (Fig. 176). It shows how similar they are and also how they vary. Some curves reach zero between one and two miles. Some curves reach zero at some distance in excess of the six miles maximum in the figure. There is a tendency for curves whose initial position is high to remain high with increased distances and to terminate at more remote distances than curves which begin in a low position. A more positive generalization, (Fig. 176), is that houseflies disperse in terms of miles. Although many flies in a dispersing population do not traverse a mile many move more than six miles.

FACTORS ASSOCIATED WITH DISTANCES OF DISPERSAL

Various factors such as species, hosts, and media are operative in affecting the distances to which organisms disperse or are dispersed. These factors vary in combinations and in degrees of intensity to influence greater or lesser distances of dispersal. Variations in amount and rates of dispersion were discussed above. Different factors, different intensities and different combinations undoubtedly affect the rates of dispersion illustrated in Figs. 44, 59, 103, and 163. Inherent characteristics of populations and of individuals and chance occurrences although originating from different factors and requiring sacrifices of individuals enable some members to survive the rigors of dispersion, to reach shelter and food, to mate and to reproduce the race. Data have been obtained on effects of some of these factors. Only a beginning has been made, however, to develop comprehension of many factors. Almost nothing is known about combinations of factors and how they influence dispersal distance. Various factors are discussed below with reference to data where possible.

ORGANISM

Dispersion Is a Process of Time.—Time, in greater or lesser amounts, is required for the dispersion of all organisms. Although some species disperse or are dispersed with great rapidity the rate of spread as affected by time is of importance. Although considerable data have been reported on time spent in dispersion more extensive studies are needed.

Movement of the crown-gall bacterium, *Agrobacterium tumefaciens* (E. F. Smith & Townsend) Conn. through segments of sunflower stems was studied by de Ropp (1948). Bacteria were placed on the upper cut surface of stem fragments and cultured *in vitro*. Results were based on the frequency with which bacteria passed through sunflower segments. A regression curve was drawn to show the percentage of tubes with bacterial colonies in relation to the interval of time between application of bacteria to the stem segments and the removal from agar (Fig. 34).

There was a rapid rate of increase in number of contaminated tubes to four hours. Between four and 24 hours there was an increase in contamination. There is poor agreement of observed and curve values.

Studies on biological control of the European corn borer, *Pyrausta nubilalis* (Hbn.), by Baker et al. (1949) showed how much dispersion of the borer parasite *Lydella stabulans grisescens* R. D. was affected by time. Although secondary, tertiary and later cycles of reproduction were discussed the effects of time were prominent. Data were taken 8, 9, 10 and 11 years after introduction of the parasite but before equilibrium had been reached. A low amount of parasitization was found at four miles and more from the release point. Preliminary plotting showed that the semi-logarithmic formula would provide a satisfactory "fit" of the observed values. The independent values, years, were transformed to logarithms for computation of regression values. Two regression curves were drawn to show the effects of distance, 3.5 and 7.5 miles, on regression (Fig. 177).

The near distance, 3.5 miles, had greater parasitization each year of the observation than did the 7.5 mile group. The regression curve for the 3.5 mile group had more curvilinearity than the curve for the 7.5 mile group. Parasites were more effective at the near distance than at the more remote distance, eight and 11 years after the introduction. Time and mass-action from greater density levels near zero distance may provide part of the explanation for the differences in position and curvature.

Increases in the amount of parasitization with time are expected occurrences if an introduced parasite is to be effective. Also, the increases in abundance of an infectious disease or insect pest from an introduction are expected to accelerate with time if the factor will be destructive. The rates of incidence of white pine blister rust disease, caused by *Cronartium ribicola* F. von Wald., were studied by Fracker (1936) who showed rates of intensification of the white pine blister rust disease after its introduction into an area.

The mosquito *Aedes albopictus* (Skuse) was shown by Bonnet and Worcester (1946) to have dispersed further within four days than at any other equal period after the release of specimens. A regression curve was drawn to show how the distance of dispersal was affected by time (Fig. 178).

The mean distance traveled per mosquito per day tended to decrease with age increase of the mosquito. Although this is an expected occurrence an estimate of the rate of decrease is given. There was little distance increase after the mosquitoes were three weeks old.

Release of *Drosophila pseudoobscura* Duda by Dobzhansky and

Wright (1943) showed how much these flies reduced their rate of dispersion with age increase. Flies averaged about five days of age on the day released but ranged between 2 and 10 days for their studies. Recaptures were made from 1 to 9 days after the release. From the data given cumulative numbers of meters traversed day by day for the released specimens were calculated. By graphic studies of these data a linear relationship was obtained through transforming the independent variable, days into logarithms. A regression curve was drawn to show the rates of distance decreases (Fig. 179).

The greatest distance flies dispersed was during the first day after release of the flies. Less and less distance was traveled each day succeeding the release day. Increased flattening of the curve suggests that after about 12 days there would be no increase in distance. Any dispersion, presumably, would occur within the ambits established the first days at large. Although two observations differed considerably from the curve values there is fair agreement, especially for the first five days after the release.

Time spent in dispersing from the release point to traps was given by Lindquist et al. (1951) for three species of flies, *Musca domestica* (L.), *Phaenicia sericata* (Meig.), and *Phormia regina* (Meig.). Numbers of tagged flies caught at all distances were recorded. Numbers of flies caught on successive days were found to have linear relationships by logarithmic transformations of data on days and on numbers of flies caught. A regression curve was drawn from antilogarithms obtained for plotting the curves in Figs. 180, 181, and 182. Logarithmic transformations gave closer alignment than did other methods tried.

Housefly, *Musca domestica* (L.), recaptures decreased rapidly until four days after the release. Most *Phormia regina* (Meig.) and *Phaenicia sericata* (Meig.) flies were also taken within four days after the release. More *P. sericata* (Meig.) were taken between four and eight days, however, than of the *M. domestica*. *M. domestica* recaptures decreased most rapidly of the three species; *P. sericata* least rapidly of the three species. There is fair agreement of observed and curve values in Figs. 180, 181, and 182.

Population Density.—Some individuals in a population disperse to greater distances than others. Part of this is attributed to inherent ability in the organism and part is attributed to more favorable positions and fortunate movements. More distant dispersion may be expected, therefore, from a dense than from a sparse population owing to these factors. Another factor, crowding, may provide stimuli for increasing the distances to which more dense populations disperse. Evaluations of different population densities in dispersal activities are needed. Consideration of initial density populations would give more understanding of biological phenomena and result in more success of economic projects. Although some attention was given to different densities earlier, Wolfenbarger (1946), as related to distance further references are given to work that has been done.

In studying maize rust epidemics, *Puccinia sorghi* Schw., Zogg (1949) observed a relationship of uredospore number and dispersion distance. Uredospores in the Rhine valley dispersed to distances depending on the number of spores in areas of production. Two regression curves

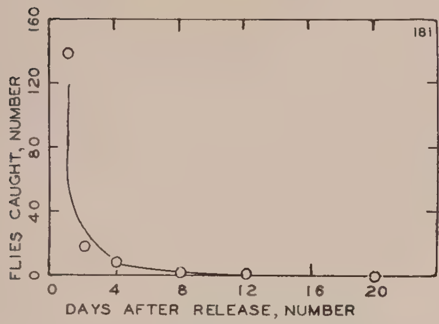

Fig. 181

Recovery of *Phormia regina* on days following the release (data from Lindquist, et al.).

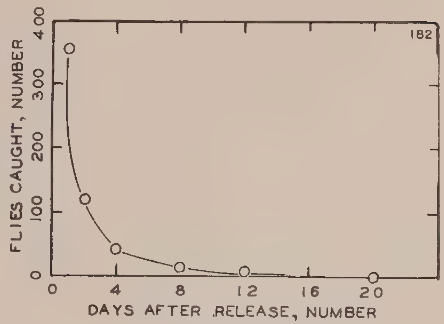

Fig. 182

Recovery of *Phaenicia sericata* on days following the release (data from Lindquist, et al.).

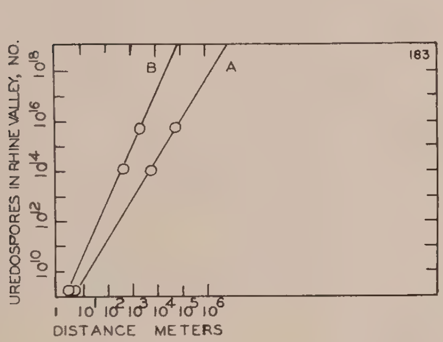

Fig. 183

Uredospore numbers at origin influence distances to which spores are dispersed.

Curve A represents valley-winds.

Curve B represents mountain-winds (reproduced from Zogg).

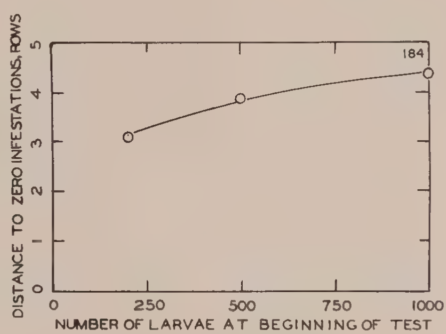

Fig. 184

Larval density dispersion and distances to which zero was reached (data from Neiswander and Savage).

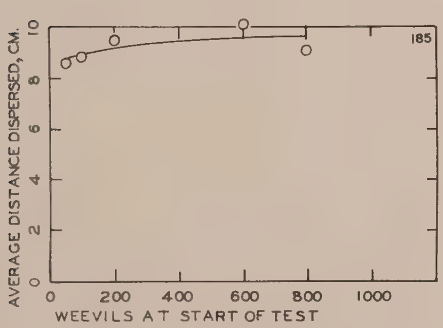

Fig. 185

Density of Azuki bean weevil and average distance of dispersion (data from Watanabe, et al.).

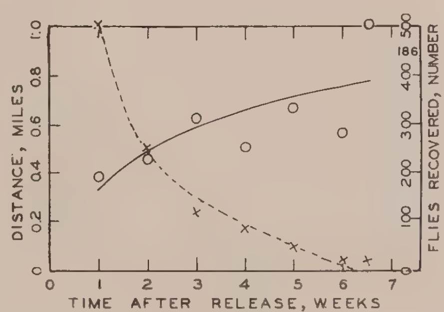

Fig. 186

Dispersion of male tsetse flies

Solid line (upward curve) represents distance to which flies dispersed.

Broken line (downward curve) represents number of flies recovered (data from Jackson).

were drawn, one illustrates the dispersion of spores by valley—the other by mountain—winds. A straight-line function was found by logarithmic transformations of the dependent and the independent variables. In Fig. 183, reproduced from Zogg's (1949) Fig. 14, the spore number is given by the ordinate, the distance by the abscissa.

Regular and steady increases in distances were shown to have been dispersed by uredospores with increases in spore number. There were steady increases by valley and mountain-winds although the valley-winds caused more distant distribution from the same number of spores than the mountain-winds. Rates of distance increase, according to the regression curves in Fig. 183, show that part of the spores in a ten billion spore area dispersed to 10 meters, while part of the spores in a 10 quatrillion spores area dispersed to approximately 50,000 meters.

The logarithmic function illustrated by Zogg (1949), Fig. 183 above, was used in further studies of author's data. Population densities at the origin were used as the independent variable, X, and the distance units as the dependent variable, Y. In studies on the Euorpean corn borer, *Pyrausta nubilalis* (Hbn.), Neiswander and Savage (1931) measured distances to which larvae dispersed for pupation. Lots having different numbers of larvae, 250, 500, and 1000 each, were observed. Regression curves were drawn to show the distances from origin at which zero larvae could be expected (Fig. 184).

A slight but perceptible curve was found in which observed and calculated values have close agreement. A four-fold increase of larvae (250 to 1000) gave 1.3 row (42 percent) increase in distance. A maximum appears to have been reached with 1000 larvae in which but little distance increase could be expected by further increases in larval populations.

In laboratory studies on dispersion of the Azuki-bean weevil, *Callosobruchus chiensis* (L.), Watanabe et al. (1952) gave average distances traversed by different populations of released weevils. A regression curve was drawn among the observed values (Fig. 185) to show the regression rate.

A slight but perceptible curve was found, from data in which close agreement of observed and curve values was lacking. A 16-fold increase in the population level (50 to 800 weevils) gave 0.94 cm. (almost 11 percent) increase in the average distance of dispersion according to the regression curve. A four-fold increase in the population level (200 to 800 weevils) gave 0.48 cm. (slightly over five percent) increase.

Extension data were given by Dozhansky and Wright (1943) on dispersion of *Drosophila pseudoobscura* Duda under field conditions, from released specimens. Average distances were determined for each of four lots of released flies. These lots contained 3051, 3297, 3840, and 4810 individuals. Averages were obtained for each lot and for each successive day to five days after the release. Studies of the data showed close relationships of initial populations and distances dispersed on the fourth and fifth days after release, although it is not illustrated. Indefinite relationships were found of the other averages. These authors reported, however, that temperatures were very important in affecting distances to which flies dispersed.

SEX

Equal or nearly equal distances are dispersed by the sexes of many species of organisms. With some species, however, distances to which one sex disperses differs considerably from the other. Although reports have been made on a number of species concerning equal or differences between distances to which the sexes disperse definitive data have been reported on but comparatively few species.

Data on sex differences and similarities were given on a chironomid fly, *Culicioides impunctatus* Goet., by Kettle (1951a). This is discussed above (Fig. 118), and shows slight but insignificant differences between the sexes. Differences in distances to which the sexes of mosquitoes dispersed were recently reported by Neilsen and Neilsen (1953) and by Provost (1952). An earlier publication, Wolfenbarger (1946), gave a discussion on sex differential pertaining to dispersal distances in which there were more reports of differences on mosquitos than on other groups.

Differences in distances to which the sexes disperse appear to be dependent on species or groups of related species of organisms. Generalizations are related, therefore, to the species or group involved. Present evidence indicates little for application to the broad field of understanding of sex differences in the dispersion of small organisms.

Organisms must be of sufficient maturity at dispersal stages for the exodus and must remain in sufficient vigor to continue their life processes at the termination of the movement, otherwise they are lost to the race. An organism that dies becomes but a mass of organic material.

STAGE

More than one stage in the lives of some organisms is adapted for dispersion. One or more stages is sessile or more sedentary than others which reduces the frequency of dispersal. The state of being sessile or sedentary, however, may or may not influence the distances of dispersal. It is of interest to understand and it is of value to economic projects to know the dispersal patterns of the different stages of an organism. Stages or phases of organisms in which dispersion occurs are important from the viewpoint of the administration of quarantine measures.

Pollen and seed are usually more dispersive than other plant parts. Although apple, *Malus pumila* L., pollen, fruit, seed and plants may be dispersed, only data giving distances to which pollen may be dispersed are known Hutson (1926), MacDaniels and Heinecke (1929), Roberts (1945), Richey (1946) and Wright (1952). Corn pollen dispersal has been studied, Bateman (1947), Haber (1935), Haskell and Dow (1951), Hodgson (1949), Jones and Brooks (1950), and Jones and Newell (1946), but no data are known that are descriptive of distances and amounts of corn that are scattered or moved about. A discussion of the role of some birds and mammals in seed dispersal and germination was given by Krefting and Roe (1949).

Most insects have three or four stages in which dispersion may occur. Eggs and pupae of the primary screwworm fly, *Callitroga hominivorax* (Cqrl.) may be moved by man, for example. Larvae and adults of the fly, on the other hand, are active in dispersion. Larvae

are widely dispersed by animals although data are not known to show it. Larvae move about feeding (although perhaps in terms of inches) and following maturity to suitable locations for pupation. Adults fly seeking food and mates. After mating the females seek sites favorable for egg deposition. Data were given which estimate distances to which larvae dispersed for pupation, Travis et al. (1940), and to which adults dispersed until they were captured, Schoof and Siverly (1954a) and Lindquist et al. (1951). An application of the dispersion habits for mating was reported by Knipling (1955) for control and eradication of the species through gammaray irradiation.

Aging of Dispersing Organisms.—It is generally accepted that aging begins with birth of hatching and continues throughout the life of the individual. Members in a dispersing population age, therefore, as they respire, reduce concentrations, move or are moved to other locations and otherwise pursue activities to maintain and preserve life. In these activities members become fatigued, age and many perish enroute to situations favorable to propagate their race. As a result organisms disperse or are dispersed shorter and shorter distances with increasing age. Although different organisms possess different life activities all possess patterns of dispersion. Certain pollens, for example, have short lives and must perform their function within minutes or hours of departure from their source or perish. Certain seeds, on the other hand, age slowly and may remain in the disperse phase of life for many years awaiting favorable media for growth and reproduction. There are data on certain active disperser organisms that show effects of aging of populations as measured by distances but none on organisms that diperse passively.

In his studies on dispersion of the tsetse fly, *Glossina morsitans* Wst., Jackson (1940) released and recaptured flies to study their movements. Data obtained show time, in terms of weeks, to recovery from release and distance, average miles covered. Two regression curves were drawn to show the results (Fig. 186).

A rapid rise during the first week after release from zero distance is indicated. After the first week less and less distance was traversed. The observed value at "over six" weeks appears to be an extreme variant and although it was used for computing the regression curve it is probably too high. Aging of flies, however, reduced the average miles dispersed so that after six weeks but little distance was covered. Numbers of flies recovered became so few that about four percent were taken at six weeks after the release. There is fair agreement of observed and curve values.

Reciprocals of distance covered (not illustrated) show that by comparisons of distance traversed and number of flies recovered there is more deceleration by average distance than by number of flies recovered. Flies were collected but were less active in the latter weeks of activities than during the first week after release. It appears, therefore, that age had retarded distance of flight more rapidly than death decimated the numbers.

Male tsetse flies, *Glossina morsitans* Wst., were also reported in a later publication by Jackson (1946) to disperse less distance with increasing age. A regression curve was drawn from these data to show age effects (Fig. 187).

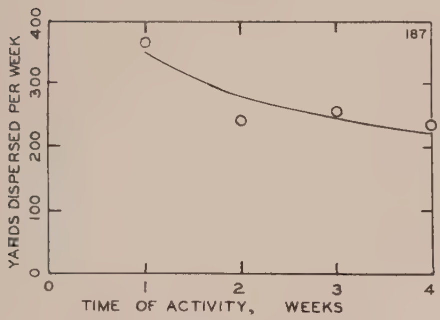

Fig. 187
Rate of male tsetse fly dispersal as affected by age (data from Jackson).

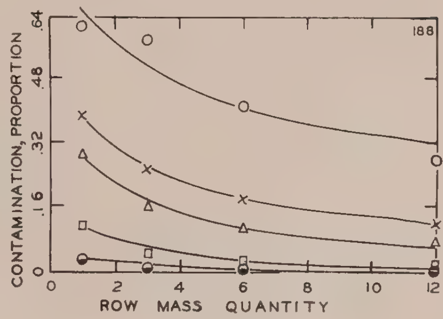

Fig. 188
Incidence of contamination from masses of plants.
Upper to lowest curves represent data taken at 1.0, 2.5, 4.5, 15.0 and 30.0 feet, respectively, from the source of the contamination (data from Bateman).

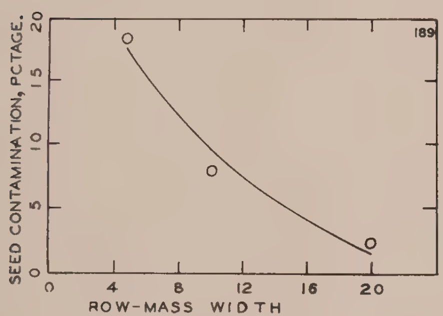

Fig. 189
Incidence of contamination in corn as affected by row number (data from Mudra, after Haskell and Dow).

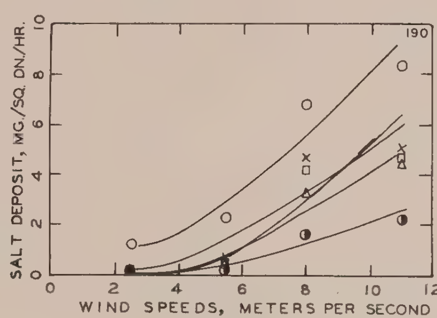

Fig. 190
Increase of salt deposits by wind speed.
Highest curve represents data taken at 20 m. from mean tide level.
Lowest curve represents data taken at 270 m. from mean tide level.
The other curves represent data taken at intermediate distances from mean tide level (data from Boyce).

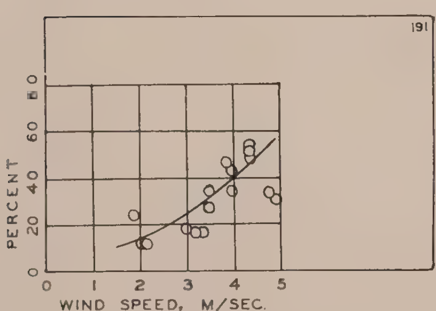

Fig. 191
Pollen deposition as related to wind speed (reproduction of Fig. 3 from Jensen and Bøgh).

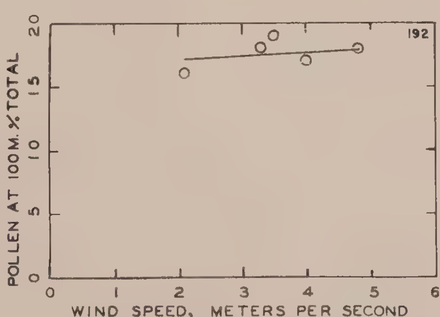

Fig. 192
Pollen deposition as influenced by different wind speeds (data from Jensen and Bøgh).

Average numbers of yards dispersed per week are shown in (Fig. 187). Accumulated yards distances given by the author were 365, 484, 772, and 941 for the 1, 2, 3, and 4 weeks of activities, respectively. Marked decreases in yards dispersed are shown with aging of the insects. After four weeks of age the flies tended to remain in one location.

Periodicity.—Organisms occasionally move from their origin at certain rather definite times. Movement may occur at rather specific hours, seasons or other times. Mass movements of swarms appear, as if at some pre-arranged signal many organisms had matured and awaited the final moment of departure. Although light, temperature, moisture and other factors undoubtedly influence periodicity the activity is not well understood. The term "rhythm" was used by Andrewartha and Birch (1954).

Dispersal of grass pollen at intervals was reported by Jones and Newell (1946). Periodicity in avocado flowering was described by Wolfe (1934). Many insects are undoubtedly active at stated periods. Aphids were reported by Broadbent (1950) as having flight periodicity. Periodicity in mosquito flights, *Aedes taeniorhynchus* Wied., was recognized by Provost (1952).

HOST

Host plant and animal density, stage, dispersal, and attractiveness affect dispersal distances of organisms. Effects of these factors vary considerably among organisms. Since the hosts are also organisms to various conditions for living multiple effects are possible for influencing life of plants or animals living in, on or in association with them.

Population Density.—Incidence of yellows virus in sugar beets was reduced by increasing the density of host populations, according to Blencome and Tinsely (1951). Close planting was suggested for increasing the yields of beets and reducing the losses by yellow virus. Rogueing infected plants was reportedly less effective than was increasing the plant population density.

Increasing the numbers of rows (mass) of radishes, *Brassica rapa* L., decreased the incidence of hybridization. Different numbers of rows, 1, 3, 6, and 12, of Scarlet Globe variety were planted at varying distances from a central source of the contaminating Icicle variety by Bateman (1947a) in order to show the effects of massed plants.

The expected proportion of hybrids calculated for the curves in Fig. 70 were taken from the 1, 3, 6, and 12 row masses at 1.0, 2.5, 4.5, 15.0 and 30.0 feet distances from the contaminant. These data were used for drawing a curve (Fig. 188). Semi-logarithmic transformations were made for the independent variables since they provided a linear relationship. The positions of the curves became successively lower in Fig. 188 as the distance increased from the contaminant source. All curves show the relationships of contamination as affected by row masses. The term "row masses" might be used instead of "pollen receptors". Similar rates of decrease were found for all curves except that as distances increased the curves tended to have increasingly less and less slope. The 30.0 foot distance, bottom curve in (Fig. 188),

for example, is nearly flat. Statistical analyses by Bateman (1947a) showed that the "row-mass" interaction was significant, thus confirming the observation that flatter regression curves may be expected at the greater distances. The pollen grains are shown to have accepted plants in the greater row-masses as restrictive barriers to more distant dispersion. Bateman (1947a, 1947b, and 1947c) gave more recognition to the subject than have previous authors.

In discussions on crowd diseases (defined as those caused by inocula which have dispersion ranges of short distances and lives of short duration in the soil) van der Plank (1948a, 1949a, and 1949b) emphasized the importance of larger and fewer fields as favoring less loss from plant diseases. Specific diseases such as groundnut rosette disease, maize streak disease and aphid borne virus diseases of beet were considered of less importance if fields were larger and fewer. Inocula of crowd diseases from outside the fields would move slowly into the fields and on a per acre basis the amount of disease would be much less than with many very small fields of equal area.

Absorptive influences of multiple numbers of corn rows are illustrated by data from Muda (1943 after Haskell and Dow [1951]). The amount of contamination of middle rows became successively less and less with increased row-mass width plots. A regression curve was drawn to show the seed contamination as related to row-mass width (Fig. 189).

A rapid decline in seed contamination is shown in plots from 5 to 20 rows wide. A zero contamination may be expected, according to the regression curve, at near 23 feet. There is fair agreement of observed and curve values.

Increased density of host plants, or absorption of dispersing pollen by barrier rows has been used by corn breeders for many years. Less contamination may be expected from absorbent masses of plants, according to Muda (1943, after Haskell and Dow [1951]), than from spatial isolation. Further research in the field may reveal that very significant discoveries may be obtained from increased host densities.

Small cotton fields separated by considerable distances were reported by Hunter (1910) to cause more dispersion of the cotton boll weevil, *Anthonomous grandis* Boh., than large and extensive fields of heavy cotton production. Dense populations of cotton plants were believed to absorb the insects while crowding caused by dense populations in small fields motivated the beetles to flee further.

STAGE

Different stages of plants or animals of the same species usually serve as agents of dispersion or as hosts to different species of organisms. Examples illustrating this are comparatively few.

Potato viruses are transmitted by winged and wingless aphids. Winged aphids were considered by Broadbent and Tinsley (1951) and by Simpson (1953) to disperse virus inoculum more distantly than do wingless aphids. Wingless aphids, however, served to intensify infections among neighboring plants.

Infestations of the Florida red scale, *Chrysomphalus aonidum* (Linn.), may be found on orange, *Citrus sinensis* (Linn.) Osbeck, fruit

and on foliage of grove and nursery trees. Fruit is shipped to distant locations more commonly than are trees and might be expected to transmit new infestations more than trees. There is apparently no evidence, however, indicative of distances to which either stage of the orange may have dispersed the scale.

DISPERSAL

Host plants dispersal may be one of the more important means of spread of viruses, bacterial or fungal diseases and of insect pests. Part of such dispersal may be as conducted by an agent, wholly mechanical and outside the province of the above heading. Host organisms, on the other hand may serve an obligate biological need for an organism (or virus material) and at the same time serve as a means of dispersal.

Incidence of virus diseases came under this heading as given in Part 1. Pollen dispersal of many plants is accomplished by insects and depends on the dispersal of the insect involved. Distances to which the pollen is dispersed are also given in Part I.

ATTRACTION

Active dispersive organisms are recognized as having power to be drawn or attracted to an objective or to one another. Although movement is made through germination and growth of passive dispersive organisms such action does not transfer the organism from one site to another. Actively dispersing organisms, however, exhibit purposeful movements. Such movements may be activities separate from responses to crowding, temperature, age, wind, sunlight and certain other factors. It is often difficult or impossible to determine and classify movements as to attraction, repulsion or chance position. It may be questioned whether all movements are not responses to motivations which have purpose. It appears that repulsion and attraction are important activities since active dispersive organisms are recognized as seekers or searchers for food, shelter or protection and mates. A third classification may be that as the result of attraction or repulsion organisms are situated in a particular site at a particular time. Such situations may be either favorable to continued life or unfavorable and result in death to the individuals.

Attraction and repulsion may be determined through responses on the part of the organism. Baits are used for attracting flies (Figs. 126, 131, 134, 135, and 137). Examples of attractants are given for the tsetse flies (Fig. 138). Insects, especially the honeybee, influence fruit and seed yield (Figs. 156, 160, 161, 164, and 165). Attractiveness of the bloom provides stimuli for movement to nectar bearing structures. Bees collecting pollen are also attracted to pollen bearing structures.

Trap crops are occasionally recommended for use in the control of specific insect pests. Pests are expected to be attracted to the trap crop where they may be destroyed or where they may remain innocuous.

MEDIUM

Organisms must pass through a medium or a combination of media however they disperse. Air, water and soil are the media through which organisms disperse. Examples of environments through,

around or among which organisms disperse include fields, forests, orchards, residences, shops, logs, bags of flour, factories. All media and many environments through which organisms disperse offer more or less resistance. Dispersion processes require energy from one source or another to overcome resistance to move, for maintenance of motion and for life during dispersal. With the expediture and termination of the energy supply the dispersion process may cease and the individual may perish. Various characteristics of the medium and of the environment may hasten or retard the dispersion process. Successful dispersal movements are related to the total conditions rather than to an individual component of the media or of the environment.

AIR

Air is the most common and the most important medium through which small organisms disperse. Components of the air are required in the respiratory processes of all organisms, hence, must be present for the maintenance of life. Universality of these components essentially necessitates stating a medium other than air if there is another. As a rule more distant dispersion is accomplished by air than by water or soil. All organisms are dependent on soil or water for support, however, during most of their existence. Aerial existence is a transient interlude between two local sites for most organisms.

WATER

Water, although an agent of dispersion, by its presence or absence may hasten or retard distances to which organisms may disperse or be dispersed. Water may also be a requirement for growth and maintenence of life of organisms dispersed by means of all agents. Water currents, such as rain, streams such as rivers, irrigation water and ocean currents are agents of dispersion and carry organisms from their origin. Rainfall during spore production periods was suggested by Wilson and Baker (1946) as a factor reducing distances to which conidial, spores of *Sclerotinia laxa* Ader. and Ruh. were dispersed by wind. A relationship was reported by Brown (1951) in which species of Corixidae frequenting temporary bodies of water had a higher rate of migration than species frequenting permanent bodies of water. Reference to "Moisture" below is regarded as a separate function and refers to air or soil rather than to water.

SOIL

Soil inhabiting organisms are represented by very few definitive data on dispersion. Less is probably known of the dispersion of bacteria, fungi, insects and nematodes than of air-living organisms.

Data on incidence of damping-off disease, caused by *Rhizcotonia solani* Kuhn, were given by Blair (1943), (Fig. 15). Data were given for each of two soil types in which differences in incidence rates were evident. Although water, temperature and other factors may have influenced the incidence of disease the soil types, *per se*, were undoubtedly of importance. Most carrot rust fly, *Psilia rosae* F., larvae dispersed between one and two yards for pupation, according to Petherbridge and Wright (1943). Soil types are not known, however, to

alter distances to which mature larvae disperse. Soil inhabiting organisms generally appear to exhibit short distance ranges over which their dispersal occurs. Differences in weight-per-volume mass of the media may account for part of the shorter distance range. More resistance by soil particles, however, must require more energy per unit of distance dispersed than air or water media and is thus more restrictive of movement.

TEMPERATURE

It is recognized that the general activity of most organisms is accelerated with rising temperatures. Optimum temperatures exist for all organisms and would appear to favor optimum dispersal. Extremes of temperatures may be expected to limit more distant dispersal by direct and indirect means. High and low temperatures may affect dispersal distances of various organisms, but reports of these have been of a qualitative rather than of a quantitative character. Reviews of relationships of weather, including temperature, were given by Foister (1935, 1946) with reference to fungus diseases of plants and by Uvarov (1931) with reference to insects. Temperature influences the production and germination of spores and pollen and the rate of movement of insect agents that provide transportation of some spores and pollen. Relationships of temperature and distance were measured by Dobzhansky and Wright (1943) who reported very little dispersion below 60° F. for *Drosophila pseudoobscura* Duda. Increased temperatures above 60° F. were calculated by these authors to increase the distance (based on regression) by 760 m^2 per degree. Temperatures of 80° F. were found by Parker et al. (1955) for initiation of flight of the migratory grasshopper, *Melanoplus mexicanus* (Saus.).

Temperatures below the optimum are a pre-disposing factor reducing and retarding production of small organisms. With the onset of higher temperatures the production of organisms is resumed and movement is accelerated. Low temperatures if existent for but a short time may have no significant influence on the final distance of dispersal. High temperatures may accelerate the production and dispersal rate by reduction of the life span of the disperse phase. High temperatures bring about outward quiescence on the part of some organisms so that dispersal is retarded.

Moisture.—Extremes of moisture in air and soil have major effects in the lives of most organisms. A number of fungal spores perish in moist conditions but have a higher rate of survival under dry conditions, according to Foister (1946). It is conceivable that more distant spore dispersal may occur under dry conditions owing to longer life and that shorter distances may be covered during moist or wet weather. Evidences for verification of this conception, however, are not known.

Dispersal activities of the potato leafhopper, *Empoasca fabae* (Harr.) were observed by the author in earlier unpublished studies, during wet or rainy periods. More leafhoppers appeared to be flying in daylight hours in wet rainy weather than in daylight hours on cloudless days although no data were taken for comparisons. More frequent biting by mosquitoes during wet periods is a common experience.

Since higher moisture periods are so commonly associated with lower temperature and with hours of darkness it is practically impossible to separate the effects of the different factors. As a result definitive effects appear not to have been determined for moisture and its effects on distances to which dispersal of organisms occurs. Many active disperser organisms, however, choose an optimum moisture range where they are afforded an opportunity, according to the literature review by Andrewartha and Birch (1954).

Tsetse fly activities are favored more by wetness and water than by dry locations. Ruined compounds were more frequent nearest rivers where tsetse flies were present, according to Morris (1952) (Fig. 139). Tsetse flies moved greater distances to attack their host animals during the wet than during the dry season. Tsetse flies, *Glossina morsitans* Wst., were reported by Jackson (1940) to live longer during the rainy season than during the dry season. More distant dispersion, therefore, might be expected in the rainy than in the dry season.

LIGHT AND DARKNESS

Most organisms are more active and most dispersion is probably accomplished during daylight hours. Ejection of spores and seeds is probably more frequent in daylight hours than in hours of darkness. More distant dispersal may occur after fruit bodies become dry in daylight hours than may follow periods in which fruit bodies remain damp or wet. Sporangia of *Phytophthora infestans* (Montagne) de Bary were dispersing in abundance between 8 A. M. and 6 P. M. with peak abundance between 9 A. M. and 12 noon, according to Bawden (1952). Pollen of grasses was found by Jensen and Bøgh (1941) and by Jones and Newell (1946) to disperse in daylight hours. Weeping lovegrass, *Eragrostis curvula* Schrad and Nees, was shown by Jones and Brown (1951) to shed most pollen about sunrise although some had been shed in the darkness previous to sunrise. Six other grasses, Tall fescue, *Festuca elatior* var. *arundinacea* (Schreb.) Wimm,; bromegrass, *Bromus inermis* Leyss; rye, *Secale cereale* L.; Johnson grass, *Sorghum halepense* (L.) Pers.; sweet corn, *Zea mays* L. and switchgrass, *Panicum virgatum* L.; however, shed all their pollen in daylight hours. More tree pollen was reported by Rempe (1937) from daylight aeroplane flights than from night flights. Pollen "drift", however, was greater, percentage-wise, during day than night hours. Since there are fewer and less turbulent air currents at night than at day it is suggested that there is more drift of organisms in daylight hours than in hours of darkness.

Insect activities vary considerably with daylight and darkness. Aphids take wing from the host plant principally in daylight hours, according to Johnson (1951, 1952). The beet leafhopper, *Circulifer tenellus* (Baker), was found by Lawson et al. (1951) to be in flight most abundantly about sunset although many insects took flight shortly after sunrise. A staphilinid beetle, *Paederus fuscipes* Curtis, was reported by Scott (1950) to have a tendency for flight at night. Flights of the migratory grasshopper, *Melanoplus mexicanus mexicanus* (Saus.) began on clear days, most often between 11 A. M. and 1 P. M. and ceased abruptly when clouds obscured the sun, according to Parker et al. (1955). Of 912 cotton-boll weevils, *Anthonomous grandis* Boh., caught

by Fenton and Dunnam (1928) on adhesive covered screens, 490 were taken in the forenoon, 367 in the afternoon and 55 were taken at indeterminate hours. Many species of Lepidoptera fly at twilight and in the hours of darkness. Larvae of the first instar of the gypsy moth, *Porthetria dispar* (L.), were most active in dispersion between 2:00 and 5:00 P. M. although a secondary peak of dispersing larvae occurred between 10:00 and 11:00 P. M. according to Minott (1922). Diurnal activities of the fruit fly, *Drosophila pseudoobscura* Duda were reported, by Mitchell and Epling (1951) as most abundant in late afternoon and early morning hours. They reported also that the effective seasonal migration for any particular locality was determined by the interactions of a number of factors including (1) the diurnal and seasonal cycles of light activity, (2) the diurnal and seasonal cycles of temperature, (3) the seasonal cycle of population density and (4) the seasonal variation in the nature and distribution of feeding and breeding sites. A reduction in the number of honeybees returning to the colony abode with approaching darkness was reported by Ribbands (1951). The ". . . influence of the sun on flight direction" was reported by Lindroth (1953) as most individuals of *Oodes gracilis* Villa went west rather than east. Such observations are reported but rarely.

Directional Influences.—Air currents are expected to influence the direction of dispersal of many organisms. This is especially true of organisms that disperse passively, such as spores, seeds, pollen and many insects. Although a discussion of directional influences was given earlier, Wolfenbarger (1946), available evidence continues to show that winds do influence directions to some degree to which organisms are dispersed but that such influences appear more temporary and localized than general. Effects are generally matters of degree rather than of an all or none character. Prevailing winds occur in almost every locality but records of performance of dispersion process usually indicate that influences are provided to disperse organisms in all directions. Plant breeders, for example, depend on distance rather than direction for insolation and maintenance of pure lines. Seed potato growers depend on distance rather than direction from virus sources to maintain plants as free of virus inoculations as is practical.

WIND

It is inevitable that winds would influence the dispersion of some organisms. Passive disperser organisms, for example many spores, seeds, pollen, some insects, and mites, depend on the turbulence of air currents to move them about. Many active disperser organisms, like many insects, on the contrary retard and postpone flight movements during strong or turbulent winds. Insects appear to retain control of their movement, hence, the reduced flight movements. Less biting by mosquitoes during strong, 15-up miles per hour, winds is a common experience in areas where mosquitoes are abundant.

Wind speed affected salt deposits from sea-water as shown by Boyce (1954). Although it is expected that greater wind speeds would carry water droplets further than lesser wind speeds the rates are illustrated by regression curves, from data given for 20, 45, 95, 120 and 270 meters from mean low tide salt deposits given for different wind speeds (Fig. 190).

Similar curvilinearities are shown by the observations except for those at the 95 meter distance. A steeper slope of the regression curve is shown by the data from the 95 meter distance. Winds of 11 meters per second, for example, carried eight milligrams of salt per square decimeter per hour at 20 meters from mean low tide. Winds of the same speed carried three milligrams of salt per square decimeter per hour at 270 meters from mean low tide.

Wind speed, meters per second, appeared to have had curvilinear relationships with salt deposits and were calculated on that basis. Greater wind speeds deposited more salt water droplets than lesser wind speeds. Correspondingly greater deposits resulted from greater wind speeds.

Although different wind speeds are expected to influence pollen deposition there are but few comparative data taken under field conditions which measure wind speed influences. Considerable attention was given to wind speeds and their rate of influence by Jensen and Bφgh (1941). Stronger wind speeds were shown to have deposited considerably more pollen at 100 meter distance than weaker winds. A reproduction of Fig. 3 from Jensen and Bφgh (1941) is given (Fig. 191).

Rather marked differences are shown, illustrating that higher wind speeds carry a bigger percentage of the pollen further than weaker winds. A curvilinear function was shown for wind speed and pollen deposition. Influences were measured in percentage terms of pollen grains at 100 meters as compared with those at 0 meter from data given by Jensen and Bφgh (1941). Another means of comparison was used in which percentages of pollen at 100 meters were calculated as of the total of pollen from all distance classes. A curve was drawn to show the results (Fig. 192).

A much flatter curve resulted from this method of comparison. There is much less influence from different wind speeds than is shown in Fig. 191. A question arises, therefore, regarding methods of comparison, i.e., whether to base influence of wind speed on the pollen deposition data at zero distance, (Fig. 191), or on data over the distance range.

Collection of aphids by suction-traps and tow-nets were made by Johnson (1951) to determine comparative densities at various wind speeds. From the illustration given by the author data were obtained for drawing a regression curve (Fig. 193).

Rapid decreases in aphid density were found with increases in wind velocities. These decreases reached a low density at near eight miles per hour. In consideration of the observed densities from two to seven miles per hour a curve might be drawn that possessed a slight curvature and reached zero density at near seven miles per hour. The observed densities at eight, nine and ten miles per hour were very low. A wind speed of nine miles per hour may be near the speed at which aphids initiate flight.

Although it is a generally accepted statement that insects fly at calm or low wind velocity periods and that they remain at rest in protected places during windy weather, very few definitive data are given to show the effects of different wind speeds in keeping insects at rest. Other factors, maturity of host plant and insect for example, may provoke insect departures from rest and give rise to initiation of

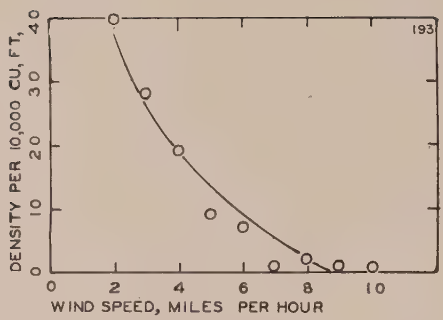

Fig. 193
Density of aphids at different wind speeds (data from Johnson).

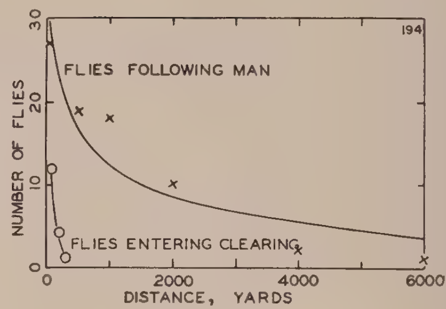

Fig. 194
Incidence of tsetse fly attacks (data from Swynnerton).

flight during severe winds. The observed data in Fig. 193 above of low densities at higher wind speeds suggest that low densities approach but reach zero at higher and unknown wind speeds. The comparative term "frequency" rather than "abundance" or "density" may be more descriptive of the populations at the highest wind speeds.

Studies by Johnson (1951) showed a diurnal periodicity of flight and a nocturnal quiescence at low altitude levels. Insect density at higher levels (thousands of feet) was believed to coincide with convection and turbulence.

BARRIERS

There are barriers of different types and different degrees of restraint. These have varying degrees of effectiveness of organismal dispersion, as indicated above. Restriction of dispersion by barriers implies (1) crowding of populations into smaller areas, or (2) decreasing the movement of organisms in certain directions and increasing dispersal in others. Topography and vegetation were credited by Dowdeswell et al. (1940) with limiting the presence of species.

Topography.—Although topographical characters influence distances to which organisms disperse it is frequently difficult to distinguish between dispersal and distribution. Evidence is available, however, which shows that geographical and topographical features affect dispersal of organisms.

Observations by Parker-Rhodes (1949, 1950) on basidiomycetous fungi showed inbreeding of *Panaeolus campanulatus* (L.) Fr. on islands off the mainland. Two miles separation was sufficient barrier to prevent genetic interchange of island with mainland populations. Quantitative measurements of the barrier distances were discussed by Parker-Rhodes (1951) in relation to the immigration of genes into partially isolated populations of anemophilic Basidiomycetes. Off-shore islands permitted detailed studies for comparisons of species and heterozygosity of populations.

White pine blister rust, *Cronartium ribicola* F. von Wald, infections were found skewed by Buchanan and Kimmey (1938) in which more disease was, ". . . down the slope . . ." from the source of sporidia. Pollen of some forest trees, elm, *Ulmus americana* L., *Cedrus atlantica*

Manetti var. *glauca* Carr., and pinyon, *Pinus cembroides* Zucc. var. *edulis* Voss, was reported by Wright (1952) as more frequent in downhill than in uphill directions. Barriers were reported by Guppy (1917) to thwart dispersing plants. Plant dispersal throughout the world was reported by Ridley (1930, after Cain [1944]), however, as a delayed process rather than as a blockade.

A discussion by Williams et al. (1942) was given to the orientation on insects in migration. They reported that (1) strong side winds might divert directions but that the main flight directions were independent of wind directions (2) there is insufficient evidence to credit sight with influencing direction of migration and (3) there were no field observations nor experimental data to support evidence that any magnetic field influenced direction of dispersal.

Straight lines of flight were maintained by the painted lady butterfly, *Vanessa cardui* L., regardless of topographical features according to Abbott (1950). Each butterfly kept a few feet above trees, the ground, building and other objects as it flew unswerving on its way. Individuals arose to considerable heights to fly above tall trees, buildings and other objects rather than circumnavigate an object by deviation of a few feet.

One of four aspects open for study suggested by the Committee on Quantitative Ecology, Park et al. (1941) was, ". . . the geographic movement of single species population."

Vegetation, Physical State.—Reference is made under this heading to non-host plant species, their density or sparsity, height, and to areas without vegetation as they affect dispersion. Effects of the physical states of vegetation may be attributed directly to the attractiveness or the repellancy of conditions related to vegetation. Effects may also be attributed indirectly to vegetation. Turbulent air currents, caused by irregularities of objects such as buildings and trees, were believed by Durham (1951) to hold many pollen grains in suspension until they were caught and moved upward.

Data on the effects of plant growth associations were shown by Swynnerton (1936) to influence activities of the tsetse fly, *Glossina morsitans* Wst. These flies ordinarily remain in areas that are shaded or partially shaded. Flies were shown, however, to enter clearings in search of host animals. A regression curve was drawn to show the decrease in number of flies as the distance into the clearing increased. A rapid decrease was found in which no fly might be expected further than about 500 yards from the fly-bush. There is close agreement of observed and curve values. In another set of experiments Swynnerton showed that tsetse flies followed man and penetrated an Itigi-type thicket. A regression curve was drawn to show how far the flies followed their target (Fig. 194). Most flies failed to go 2000 yards, but some followed their host to 6000 yards. Close agreement of observed and curve values, however, is lacking. Restrictions of tsetse fly populations were also observed by Jackson (1940) who reported that barriers were, ". . . determined by contact lines of vegetation types."

Effects of plant presence and absence in relation to organismal dispersion have been discussed by other writers. These are usually qualitative in character and possess interest for those working with the species involved.

APPENDIX

The regression formulae used for determining the calculated or curve values used in the figures are recorded as follows:

FIG. 1. 2.5 m./sec. wind, E=0.6955 (log x)+38.3229 (1/x) −1.6586
5.5 m./sec. wind, E=0.6369 (log x)+58.3276 (1/x) −1.4872
8.0 m./sec. wind, E=−4.1477 (log x)+5.4980 (1/x)+11.8404
11.0 m./sec. wind, E=2.7643 (log x)+95.9801 (1/x)+8.2953
FIG. 2. E=26.0975 (log x)+30.2476
FIG. 3. E=−74.1393 (log x)+3,409.0363 (1/x)+145.4370
FIG. 4. E=−49.0166 (log x)+209.6621
FIG. 5. E=−30.9246 (log x)+36.2324
FIG. 6. E=20.0341 (log x)+44.0792
FIG. 7. Upper curve, E=−44.8713 (log x) −38.9321 (1/x) +137.3551
Lower curve, E=42.1919 (log x)+83.5359 (1/x)−47.0048
FIG. 8. 1942, E=−0.1001 (log x)+1.6792
1943, E=−78.4628 (log x)+164.8791
1944, E=−76.9420 (log x)+173.3237
1945, E=−80.8466 (log x)+195.2793
1946, E=−67.3683 (log x)+184.6204
1947, E=−13.5989 (log x)+116.0083
FIG. 9. 1943, E=31.2600 (log x) +1,274.4928 (1/x) −72.4107
1944, E=−13.3281 (log x) +820.1746 (1/x) +22.8402
1945, E=42.6512 (log x) +1,175.5255 (1/x) −93.7327
1946, E=20.7023 (log x) +508.8335 (1/x) −40.6783
FIG. 10. 1943, E=−33.5547 (log x) +211.0597 (1/x) +71.1124
1944, E=−141.2048 (log x) −901.0921 (1/x) +305.0550
1945, E=−3.5346 (log x) +584.5884 (1/x) +3.5346
1946, E=−18.0377 (log x) +277.1228 (1/x) +36.9408
FIG. 11. E=−26.5744 (log x) +40.6913
FIG. 12. E=−36.9627 (log x) +100.1027
FIG. 13. E=−33.3450 (log x) +75.4278
FIG. 14. Upper curve, E=−54.6585 (log x) +100.2503
Lower curve, E=−547.0976 (log x) +1003.3586
FIG. 15. A tracing from the authors figure
FIG. 16. Upper curve, E=−55.2676 (log x) +129.8877
Lower curve, E=−54.4072 (log x) +111.4358
FIG. 17. Allottment area, E=−71.1166 (log x) +93.4883
Harwood area, E=−92.2426 (log x) +80.5390
FIG. 18. $D=\dfrac{0.135\ PO/K}{X\ 15/8}$ (Waggoners formula)
FIG. 19. Focus III, E=189.4367 −79.1146 (log x)
Focus IV, E=220.7708 −85.1611 (log x)
FIG. 20. E=40.6189 −13.7395 (log x)
FIG. 21. First bed, E=29.5096 −16.2433 (log x)
Second bed, E=69.5486 −32.1079 (log x)
FIG. 22. Variety Isaria, E=93.8049 −74.7574 (log x)
Variety Rimpaus Hanna, E=106.3591 −41.5029 (log x)
FIG. 23. 1944, E=0.0692 (log x) +696.3782 (1/x) −0.7103
1945, E=1.4888 −0.4077 (log x)
1946, E=0.1878 −0.0330 (log x)
FIG. 24. E=140.5287 −53.1900 (log x)
FIG. 25. E=218.7740 −87.1803 (log x) −124.4514 (1/x)
FIG. 26. E=160,030.2608 (log x) +954,115.3009 (1/x) −208,583.5528
FIG. 27. Seed count, E=2,344.1213 +537.0742 (log x)
Yield, E=57.3862 (log x) −49.8868
FIG. 28. E=0.2236 (log x) +0.9952 (1/x) +1.2534
FIG. 29. July 3, E=10.8259 −6.6924 (log x)
July 13, E=25.6757 −1.1377 (log x)

FIG. 30. E=74.0808 −62.0161 (log x)
FIG. 31. E=38.1424 (log x) +76.6093 (1/x) −42.8407
FIG. 32. E=−23.9337 −21.2268 (log x)
FIG. 33. E=16.9616 −6.2880 (log x) +70.1940 (1/x)
FIG. 34. E=51.6188 −14.2829 (log x)
FIG. 35. E=37.9000 −17.0616 (log x) +291.6725 (1/x)
FIG. 36. No regression formula
FIG. 37. E=13.6523 −3.4635 (log x)
FIG. 38. E=1027.1596 (log x) +102,867.1970 (1/x) −2834.8385
FIG. 39. E=9.5881 −3.8565 (log x)
FIG. 40. E=432.5284 −152.0042 (log x)
FIG. 41. E=87.4391 −94.3260 (log x)
FIG. 42. 1939, Strong wind, E=16,596.5473−5529.3529 (log x)
Weak wind, E=7,825.9976 −2437.3375 (log x)
1940, E=2973.2162 −1056.5549 (log x)
FIG. 43. E=3.7939 (log x) +796.1419 (1/x) −16.0235
FIG. 44. E=13.1685 (log x) +34.0644 (1/x) −15.9341
FIG. 45. Exposure June 12–July 5, E=13.9195 +7.7639 (log x)
Exposure July 7–Aug. 4, E=10.2509 +9.2319 (log x)
FIG. 46. E=32.0304 −13.7768 (log x) +308.7715 (1/x)
FIG. 47. E=14,634.1274 −5,250.0982 (log x),
E=14,793.9429 −5,041.8964 (log x),
E=20,997.4796 −6,859.4758 (log. x),
E=4,044.8292 −1,300.1706 (log x) and
E=8,760.5352 −2,776.8678 (log x)
FIG. 48. E=8760.7623 −2776.9621 (log x)
FIG. 49. E=25.6965 −10.8075 (log x) +127.0554 (1/x)
FIG. 50. E=134.0294 −88.9362 (log x)
FIG. 51. E=83.1910 −56.3925 (log x)
FIG. 52. E=10,896.7697 −3357.9535 (log x)
FIG. 53. E=420.0324 −234.2105 (log x) +1002.5049 (1/x)
FIG. 54. Wind 1.9 m/sec., E=1737.5875 −557.2150 (log x)
3.5 m/sec., E=2613.9549 −916.6774 (log x)
4.0 m/sec., E=1737.5869 −5572.1478 (log x)
FIG. 55. E=4.0853 (log x) +713.9453 (1/x) −12.5234
FIG. 56. E=1.3239 (log x) +152.8605 (1/x) −4.4161
FIG. 57. E=0.0009 (log x) +93.7140 (1/x) −0.7288
FIG. 58. E=8,933.9426 (log x) +169,414.0987 (1/x) −18,634.3900
FIG. 59. E=210.3291 −114.0182 (log x) −212.5840 (1/x)
FIG. 60. E=0.3402 −0.1953 (log x) +1.4672 (1/x)
FIG. 61. E=420.6989 −216.5853 (log x)
FIG. 62. E=16.8774 (log x) +22.7601 (1/x) −15.7742
FIG. 63. E=0.5442 (log x) +9.5126 (1/x) −0.9063
FIG. 64. 1947, E=33.0476 −18.4552 (log x) −29.9603 (1/x)
1948, E=17.2668 −9.2407 (log x) −22.3720 (1/x)
1949, E=31.5874 −17.1432 (log x) −9.2478 (1/x)
FIG. 65. E=143.9359 −21.4528 (log x)
FIG. 66. E=189.4473 −53.2721 (log x)
FIG. 67. E=909.7636 −255.2632 (log x)
FIG. 68. E=0.0011 (log x) +1.6673 (1/x) −0.0048
FIG. 69. E=11,612.5689 −3904.2359 (log x)
FIG. 70. One-row mass, E=−0.2648 (log x) +0.1987 (1/x) +0.4185
Three-row mass, E=0.0965 −0.0694 (log x) +0.4910 (1/x)
Six-row mass, E=0.0577 −0.0413 (log x) +0.3576 (1/x)
Twelve-row mass, E=0.0427 −0.0335 (log x) +0.2403 (1/x)
FIG. 71. Stringer EA, E=0.1050 −0.1385 (log x)
EB, E=0.2316 −0.2737 (log x)
WB, E=0.2049 −0.2614 (log x)
WC, E=0.1184 −0.1466 (log x)
FIG. 72. E=13.7491 −4.6210 (log x)
FIG. 73. E=93.0572 −46.0563 (log x)
FIG. 74. E=13.0572 −4.8082 (log x)
FIG. 75. 1943, E=79.6300 −68.4177 (log x)
1944, E=85.4238 −47.4586 (log x)

FIG. 76. $E = 87.7332 - 56.1124 (\log x)$
FIG. 77. 1950, $E = 19.5886 - 3.9364 (\log x)$
1951, $E = 12.7618 - 2.0537 (\log x)$
FIG. 78. $E = 269.7953 - 44.9503 (\log x)$
FIG. 79. 1950, $E = 2.9741 (\log x) + 27.3660 (1/x) - 4.8287$
1952, $E = 2.4913 (\log x) + 23.2998 (1/x) - 3.9859$
FIG. 80. American, 1945–46, $E = 0.5104 - 0.2879 (\log x)$
1946–47, $E = 0.6300 - 0.3521 (\log x)$
Local, 1944–45, $E = 0.2953 - 0.1649 (\log x)$
1945–46, $E = 0.5223 - 0.2908 (\log x)$
FIG. 81. $E = 1.0541 - 0.5424 (\log x)$
FIG. 82. Averages all blocks, $E = -0.1447 (\log x) + 109.9543 (1/x) + 0.0734$
Zero-rod block, $E = 28.6463 - 18.0998 (\log x)$
One-rod block, $E = 24.3897 - 14.0235 (\log x)$
Two-rod block, $E = 16.6026 - 8.0848 (\log x)$
Five-rod block, $E = 8.1214 - 3.5706 (\log x)$
Ten-rod block, $E = 5.3171 - 2.2360 (\log x)$
FIG. 83. Upland cotton, $E = 97.7488 - 10.1250 (\log x)$
Asiatic cotton, $E = 64.4040 - 23.6053 (\log x)$
FIG. 84. Taylor var., $E = 60.8111 - 23.5956 (\log x)$
Wagoner var., $E = 45.7361 - 31.1114 (\log x)$
FIG. 85. $E = 4.48 - 1.17 (\log x)$
FIG. 86. $E = 572.5687 (\log x) + 854{,}872.7156 (1/x) - 1{,}674.5049$
FIG. 87. $E = 1.8945 - 0.4173 (\log x) - 11.0656 (1/x)$
FIG. 88. 1949, $E = 563.2258 - 76.8627 (\log x)$
1950, $E = 931.2767 - 116.1292 (\log x)$
FIG. 89. $E = 1284.5494 - 131.9378 (\log x)$
FIG. 90. $E = 223.0259 - 66.9205 (\log x)$
FIG. 91. $E = 13.1279 - 18.5313 (\log x)$
FIG. 92. $E = 13.1279 - 18.5313 (\log x)$
FIG. 93. Observations A, $E = 12.4080 - 15.2009 (\log x)$
Observations B, $E = 15.7503 - 16.9328 (\log x)$
FIG. 94: $E = 64.9884 - 23.7685 (\log x)$
FIG. 95. $E = 312.8065 - 133.9174 (\log x)$
FIG. 96. $E = 1.6641 - 3.2824 (\log x) + 64.\ 5594 (1/x)$
FIG. 97. $E = 351.7766 - 17.5529 (\log x) + 27{,}415.3356 (1/x)$
FIG. 98. $E = 91.9714 - 0.4186 (\log x)$
FIG. 99. $E = 51.1597 - 20.0912 (\log x)$
FIG. 100. $E = 2.6287 (\log x) + 48.1677 (1/x) - 5.3329$
FIG. 101. 1951, $E = 7.2764 - 2.9697 (\log x)$
1952, $E = 2.5593 - 1.2236 (\log x)$
1953, $E = 3.4182 - 1.6321 (\log x)$
FIG. 102. March, $E = 1387.8939 (\log x) + 3176.1038 (1/x) - 1537.8080$
April, $E = 121.5013 (\log x) + 757.4742 (1/x) - 132.5123$
May, $E = 172{,}7801 (\log x) + 443.1272 (1/x) - 178.6248$
FIG. 103. $E = 133.7386 - 34.6287 (\log x)$
FIG. 104. $E = 74.4155 (\log x) + 768.3741 (1/x) - 131.5671$
FIG. 105. Upper curve, $E = 946.4998 (\log x) + 551{,}241.8475 (1/x) - 3378.7482$
Lower curve, $E = -50.7820 (\log x) + 5866.7958 (1/x) + 164.6989$
FIG. 106. $E = 83.4213 - 33.9083 (\log x) + 1396.7936 (1/x)$
FIG. 107. $E = 14.1753 (\log x) + 21.0458 (1/x) - 13.6907$
FIG. 108. $E = 36.8262 - 16.7324 (\log x)$
FIG. 109. $E = 116.7324 - 35.0609 (\log x) + 66.1220 (1/x)$
FIG. 110. $E = 293.7746 (\log x) + 440.8701 (1/x) - 278.9236$
FIG. 111. $E = 12.4732 - 12.0922 (\log x)$
FIG. 112. $E = 16.0164 - 1.1225 (\log x)$
FIG. 113. Mosquitoes recovered, total, $E = 5.6314 - 14.5403 (\log x)$
Mosquitoes recovered, per sq. mi., $E = 4.3991 - 17.1665 (\log x)$
FIG. 114. $E = 23.2394 (\log x) - 8.1142 (1/x) - 7.5747$
FIG. 115. $E = 2.1857 (\log x) + 5.5920 (1/x) - 2.4906$
FIG. 116. $E = 3.2813 (\log x) + 13.6991 (1/x) - 4.2505$
FIG. 117. Upper curve, $E = 76.1744 - 27.4438 (\log x)$
Middle curve, $E = 70.3960 - 25.3348 (\log x)$
Lower curve, $E = 27.2130 - 10.6705 (\log x)$

FIG. 118. Upper curve, males, E=1162.9440 −588.4547 (log x)
Lower curve, females E=832.2397 −397.0382 (log x)
FIG. 119. E=0.1107 −0.0874 (log x)
FIG. 120. E=40.0396 −23.7859 (log x)
FIG. 121. E=1.5743 (log x) +2.5332 (1/x) −1.6793
FIG. 122. E=0.1283 −0.1461 (log x)
FIG. 123. E=21.2570 −20.4758 (log x)
FIG. 124. 1943, E=20.4200 −22.9516 (log x)
1944, E=20.2642 −14.5308 (log x)
1945, E=16.0870 −5.3235 (log x)
1946, E=30.8160 −4.5382 (log x)
1947, E=20.4860 −6.4796 (log x)
FIG. 125. E=0.6517 (log x) +1.5426 (1/x) −0.6524
FIG. 126. Longer curve, E=42.9021 −56.3796 (log x)
Shorter curve, E=42.3502 −46.2160 (log x)
FIG. 127. E=1.6120 −2.0892 (log x)
FIG. 128. E=−0.000,080 −0.1744 (log x)
FIG. 129. E=0.5352 (log x) +4.9636 (1/x) −1.2382
FIG. 130. E=1.1698 −1.8287 (log x)
FIG. 131. E=7.9302 (log x) +11.2679 (1/x) −9.3038
FIG. 132. E=7.7210 −89.5659 (log x)
FIG. 133. April 30–May 15 releases, E=19.4039 (log x) +42.1131 (1/x) −1.4093
June 20–July 2 releases, E=3.3933 (log x) +8.7609 (1/x) −4.0593
FIG. 134. Upper curve, E=−0.000.433 (log x) +1.2346 (1/x) −0.2331
Lower curve, E=0.9691 −2.0679 (log x)
FIG. 135. Uppermost curve, E=74.5113 −79.1928 (log x)
Dotted curve, E=61.5664 −76.7352 (log x)
Dashed-dotted curve, E=56.4662 −69.6879 (log x)
Barred line curve, E=52.2254 −63.2157 (log x)
Lowest curve, E=34.8829 −44.5581 (log x)
FIG. 136. E=2.4072 (log x) +3.4954 (1/x) −2.5231
FIG. 137. E=339.6290 (log x) +53,337.0274 (1/x) −988.7367
FIG. 138. E=471.8891 −602.1911 (log x)
FIG. 139. E=28.7520 −28.0963 (log x) +3.5806 (1/x)
FIG. 140. Wet season, E=146.5951 −58.8115 (log x)
Dry season, E=149.1045 −72.6206 (log x)
FIG. 141. Upper curve, E=610.1399 −283.7338 (log x)
Lower curve, E=4.4365 −0.3340 (log x)
FIG. 142. E=46.2912 (log x) +3243.5437 (1/x) −123.0165
FIG. 143. Upper curve, E=77.8853 −42.5822 (log x)
Middle curve, E=68.8554 −38.0462 (log x)
Lowest curve, E=5.2902 −2.3659 (log x)
FIG. 144. E=125.9851 −199.2549 (log x)
FIG. 145. E=0.5566 (log x) +958.0219 (1/x) −2.4076
FIG. 146. E=21.2721 −13.1154 (log x)
FIG. 147. E=—1.0204 (log x) +308.8287 (1/x) −1.7430
E=−12.9161 (log x) +102.4167 (1/x) +25.1883
E=—22.2593 (log x) −33.9583 (1/x) +43.2563
E=−32.9130 (log x) −104.1573 (1/x) +62.0557
FIG. 148. 1st day, E=5.8834 −3.5817 (log x) +381.7078 (1/x)
2nd day, E=91.5888 −40.3246 (log x) −75.4153 (1/x)
3rd day, E=43.1518 −18.2799 (log x) −3.2614 (1/x)
4th day, E=21.0435 −9.0200 (log x) −7.7410 (1/x)
5th day, E=7.7723 −3.3359 (log x) +21.6026 (1/x)
6th day, E=36.2061 −15.1526 (log x) −128.5704 (1/x)
7th day, E=14.9218 −6.2126 (log x) −54.9109 (1/x)
8th and 9th days, E=6.0259 −2.3803 (log x) −17.4652 ((1/x)
FIG. 149. 1st day, E=25.1885 −11.4476 (log x) +364.1705 (1/x)
2nd day, E=35.4127 −14.5597 (log x) −19.1474 (1/x)
3rd day, E=41.1522 −17.5170 (log x) −122.6311 (1/x)
4th day, E=14.2436 −4.9577 (log x) +32.5055 (1+x)
5th day, E=16.7648 −6.8627 (log x) −39.5145 (1/x)
6th day, E=−4.0422 +2.9192 (log x) +18.7923 (1/x)

FIG. 150. 1st day, E=20.0854 −12.1138 (log x) +453.4997 (1/x)
2nd day, E=60.3408 −23.8591 (log x) +82.6917 (1/x)
3rd day, E=11.5909 −3.2571 (log x) +445.2041 (1/x)
4th day, E=10.4533 −2.8777 (log x) +232.9475 (1/x)
5th day, E=2.6974 −0.0433 (log x) +261.0292 (1/x)
FIG. 151. 1st day, E=−36.6547 +14.6349 (log x) +1318.6775 (1/x)
2nd day, E=4.5833 −2.0060 (log x) +303.8422 (1/x)
3rd day, E=8.9690 −3.3778 (log x) +63.3566 (1/x)
4th day, E=5.8188 −1.9203 (log x) +5.1701 (1/x)
5th day, E=0.2784 −0.2206 (log x) +15.5008 (1/x)
FIG. 152. Upper curve, E=0.0924 −0.0200 (log x)
Lower curve, E=0.0292 −0.0064 (log x)
FIG. 153. Upper curve, E=3.2473 −1.0339 (log x)
Lower curve, E=0.9539 −0.3071 (log x) −0.4217 (1/x)
FIG. 154. E=8.3199 −3.5709 (log x) +668.5310 (1/x)
FIG. 155. Leaf mines per leaf, E=152.3708 −50.6919 (log x)
Yield, bu. per acre, E=131.2942 +28.5678 (log x)
FIG. 156. 1943, E=−4.4700 −4.7559 (log x) +28.8525 (1/x)
1944, E=8.1809 −22.1342 (log x) +3.5061 (1/x)
FIG. 157. E=145.3114 (log x) +339.7618 (1/x) −176.2193
FIG. 158. 1943, E=48.4693 (log x) +162.6842 (1/x) −65.9459
1944, E=34.4154 (log x) +49.1265 (1/x) −32.0671
FIG. 159. Hour 8:30, E=1876.3064 −0.3094 (x)
Hour 8:45, E=746.9005 −0.1399 (x)
Hour 9:00, E=113.5144 −0.0321 (x)
FIG. 160. E=968.3532 −229.9457 (log x)
FIG. 161. E=17.3196 −0.0067 (x)
FIG. 162. E=74.3333 −0.009,750 (log x)
FIG. 163. E=14.5369 −2.6578 (log x)
FIG. 164. Upper curve, E=0.6834 +0.0123 (log x)
Lower curve, E=33.7781 −1.7488 (log x)
FIG. 165. Solid line, E=46.5808 −12. 1758 (log x)
Barred line, E=160.4024 −45.3187 (log x)
FIG. 166. E=−4086.7940 (log x) +47,612.2080 (1/x) +12,876.6323
FIG. 167. E=1434.7158 −1.7595 (x)
FIG. 168. Upper curve, E=1414.6670 −287.9223 (log x)
Lower curve, E=1,116.1372 −320.5572 (log x)
FIG. 169. E=1533.6119 (log x) +55,442.6624 (1/x) −3640.9924
FIG. 170. Upper curve, E=1.3075 (log x) +140.3175 (1/x) +5.0039
Lower curve, E=−2.6572 (log x) 34.6717 (1/x) +7.8951
FIG. 171. E=610.2579 −187.5835 (log x)
FIG. 172. E=4.5115 −2.4210 (log x)
FIG. 173. E=64.3219 −45.9611 (log x)
FIG. 174. Solid line curving downward, E=48.0985 −32.1359 (log x)
Solid line curving upward, E=55.3105 (log x) −192.7897 (1/x) +2.9591
Dotted line curving upward, E=54.0391 (log x) −150.2490 (1/x) −0.0360
FIG. 175. Given previously, Wolfenbarger (1946) or in Part I above
FIG. 176. Given previously, Wolfenbarger (1946) or in Part I above
FIG. 177. At 3.5 miles, Log E=3.3317 +0.2199 (log x)
At 7.5 miles, Log E=3.1195 +0.1909 (log x)
FIG. 178. E=—33.0712 (log x) +27.7810 (1/x) +44.5462
FIG. 179. E=53.3626 +42.0344 (log x)
FIG. 180. E=2.9463 −2.2863 (log x)
FIG. 181. Log E=1.9174 −1.5775 (log x)
FIG. 182. Log E=2.5257 −1.4591 (log x)
FIG. 183. Reproduced from Zogg (1949)
FIG. 184. Log E=0.2193 (log x) −0.0096
FIG. 185. Log E=0.0368 (log x) +0.8789
FIG. 186. Distance to which flies dispersed, E=0.3311 +0.5456 (log x)
Number of flies recovered, E=471.8891 −602.1911 (log x)
FIG. 187. E=345.6835 −204.1255 (log x)

FIG. 188. 1.0 ft., E=0.6607 −0.3173 (log x)
2.5 ft., E=0.3886 −0.2513 (log x)
4.5 ft., E=0.2762 −0.2018 (log x)
15.0 ft., E=0.1095 −0.0933 (log x)
30.0 ft., E=0.0364 −0.0328 (log x)
FIG. 189. E=35.8461 −26.2461 (log x)
FIG. 190. 20 m. distance, E=32.9953 (log x) +43.8706 (1/x) −29.5037
45 m. distance, E=23.2847 (log x) +30.5350 (1/x) −21.3602
95 m. distance, E=38.9330 (log x) +62.6805 (1/x) −40.1062
120 m. distance, E=22.7087 (log x) +31.2232 (1/x) −21.6535
270 m. distance, E=10.7515 (log x) +15.1268 (1/x) −10.2780
Fig. 191. Reproduced from Jensen and Bøgh (1941)
FIG. 192. E=16.7809 +0.1460 (x)
FIG. 193. E=54.8835 −58.8359 (log x)
FIG. 194. Flies following man, E=51.9341 −12.9765 (log x)
Flies entering clearing, E=58.8611 −23.5436 (log x)

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INDEX TO SPECIES

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